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TREATISE

ON

HUMAN PHYSIOLOGY.

FOR THE USE OF

STUDENTS AND PRACTITIONERS OF MEDICINE.

BY

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PREFACE TO SECOND EDITION.

In submitting a revision of his Treatise on Human Physiology to the profession, the author may say that its fundamental plan remains unchanged, as continued experience in teaching confirms his belief in its adaptation to the needs of both students and practitioners, two classes whose demarcation is really artificial.

Aside from its plan the book has been recast. The recent advances in our knowledge of Physiology, especially of Physiological Chemistry and of functions of the Nervous System, have necessitated the rewriting of a great part of the work and the addition of new illustrations. The author has endeavored to accommodate these important additions without an increase in the number of pages, by the most careful condensation and elimination of less important matter, and he trusts that his efforts to make the work more than ever useful as a text-book have not been without beneficial results.

It need hardly be said that the additions made here and there to the bibliography (always obtained from the original sources quoted) represent but a selected part of the vast Physiological literature that has appeared in the last few years, but it is hoped that no important additions to our knowledge of the subject have been omitted.

HENRY C. CHAPMAN.

Philadelphia, April, 1899.

PREFACE TO FIRST EDITION.

To those familiar with the many excellent German, French, and English treatises upon Physiology, it may appear strange that the author should feel it incumbent upon himself to offer one more contribution upon such a well-worn theme. The experience, however, of the past eight years, as Professor of the Institutes of Medicine or Physiology in the Jefferson Medical College of Philadelphia, has convinced the author that there is a want felt by students and practitioners of medicine for a systematic work, representing the existing state of physiology and its methods of investigation, and based upon comparative and pathological anatomy, clinical medicine, physics, and chemistry, as well as upon experimental research. It is the hope of the author that the present work, embodying essentially his teaching, will not only supply such a want, but will facilitate and stimulate the study of this most important branch, the institutes, that is to say, the foundation of all rational medicine. The author takes much pleasure in here expressing his acknowledgments to Dr. A. P. Brubaker, Demonstrator of Physiology in the Jefferson Medical College, for the assistance rendered in the performance of the experimental part of the work; to Arthur E. Brown, Esq., Superintendent of the Zoölogical Garden, of Philadelphia, for the many facilities and courtesies extended in the dissection of the rare animals that have died at the Garden, the results of which are frequently made use of in the work, and to Dr. Lawrence Wolff, Demonstrator of Chemistry in the Jefferson Medical College, for the favor of seeing the work through the press.

HENRY C. CHAPMAN.

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PHYSIOLOGY.

INTRODUCTION.

Physiology, from the Greek φυσις and λογος, literally means a discourse on Nature. At the present day, however, the word has not such an extended significance, physiology as understood by naturalists and physicians meaning the study of the functions or uses of the parts of which living beings consist.

The word parts is used in preference to that of structures, inasmuch as there are beings like the monera, simple masses of a jelly-like substance or protoplasm, which are so structureless and unorganized that great difficulty is experienced in classifying them, it being questionable whether they should be ranged among plants or animals, or relegated to an intermediate kingdom, the "Protistenreich" of Hæckel,[1] or, as Huxley[2] expresses it, a sort of a biological "no man's land." Indeed it has been doubted whether the term living at all could be properly applied to the monera in the same sense in which that word is used in reference to the higher animals. As the totality of the functions or uses of the parts, structures, or organs of which living beings consist, constitute their life, Physiology may be defined therefore as the study of life or of function.

Necessarily from the definition, Physiology presupposes a knowledge of anatomy or structure. The relation of the two may be compared to the study of a clock when at rest and when going.

The anatomist studies the form and relation of the weights, the pendulum, the hands, etc., at rest; the physiologist, the fall of the weight, the swinging of the pendulum, the movement of the hands. Anatomy is the statical, physiology the dynamical, part of biology.

As well might the mechanician hope to understand the movements of the clock and to regulate it without a knowledge of the parts composing it, as for the physiologist to understand the motions of the living body without a previous knowledge of its structure.

Anatomy and physiology are so intimately associated that, philosophically, they should be studied together; indeed, to separate them, except for the convenience of teaching, is highly illogical.

As Hyrtl[3] well observes, "Anatomy, unassociated with physiol-

[1] Generelle Morphologie, Bd. 2, s. xxii. Berlin, 1866.
[2] Physical Basis of Life, p. 129. Lay Sermons. New York, 1871.
[3] Lehrbuch der Anatomie, s. 18. Wien, 1881.

ogy, is a mindless study and does not deserve the name of science. Can one study the arrangement of a machine without any reference to its object? It is possible simply to view the harmoniously arranged parts of a whole, simply to stare at it without reflection. The anatomist can undertake no investigation without considering the physiological questions involved. The paths of both sciences meet and cross each other in so many places that there are but few divergent points."

In beginning the study of any subject not only is it indispensable that the object of the investigation should be clearly defined, but it is proper that relation to knowledge in general should be pointed out.

The classification of the sciences has been a vexed one from the time of Bacon [1] to Comte.[2] This, from the nature of things, might have been expected; for there are no sharply defined lines in nature; one science encroaches so upon another that it is impossible to say where the one ends and the other begins. All classification, therefore, must be imperfect. The following one, that of Comte, is open to many criticisms, as shown in the masterly essay of Spencer.[3]

Classification of Knowledge:

- Mathematics.
- Astronomy.
- Physics.
- Chemistry.
- Biology.
  - Botany.
  - Zoölogy.
    - Anatomy.
    - Physiology.
- Sociology.

Admitting its many faults, we make use of it here on account of its brevity simply to indicate the position of Physiology relatively to that of other kinds of knowledge.

It will be seen, from the table, that the study of plants and animals constitutes the subject-matter of Biology.

The second division of this grand science comprehends all that is known of the structure, functions, habits, geographical and geological distribution of animals; therefore, the study of animal functions or animal physiology is a subdivision of Zoölogy. In the same manner, vegetal physiology forms a part of Botany. Human physiology, a part of general animal physiology, forms the subject of this work.

If the sciences are studied in the order in which they follow each other as given above, then the inorganic will precede the organic. This is the logical order and historically the one in which they were, generally speaking, cultivated, for the phenomena of the inorganic world are less complex and more easily generalized than those of the organic, and, therefore, more readily investigated.

[1] De Augmentis Scientiarum. [2] Cours de Philosophie Positive.
[3] Genesis of Science. Essays. London, 1868.

Wherever practicable, the historical order will be found to be the best one to pursue in the study of any science; indeed, as we proceed, it will be seen that the phenomena of physiology depend upon physical and chemical laws, and that probably, with the advance of knowledge, the whole subject will be treated as a branch of molecular physics—hence the indispensability to the student of physiology of a knowledge of physical and chemical science. Ample illustrations of the value of such knowledge will be given when the special functions are considered. The special senses of sight and hearing, for example, depend for their successful study upon familiarity with optics and acoustics; the investigation of the circulation is a question of hydraulics; that of secretion, of organic chemistry.

By referring to the classification just offered, it will be observed that Botany comes before Zoölogy; where practicable, its study should precede that of Zoölogy, for plants serve to bridge over, to a certain extent, the gap between the mineral and animal worlds, and at different points touch the confines of these two kingdoms. Further, with some exceptions, plants are destitute of a nervous system, and even if extended investigation should show that their nervous system is more developed than now it is supposed to be, it would exercise a small influence as compared with that of the higher animals. Plants, therefore, offer a favorable opportunity of examining the processes of nutrition uninfluenced by the nervous system.

When we come to examine the circulation, digestion, etc., in man, we shall see that these functions are greatly modified by the nervous system; hence the advantage of studying nutrition in lower organizations where these disturbing elements are eliminated.

Having endeavored to define the object of our study, and to indicate its limits and relation to knowledge in general, let us now consider the different methods by which human physiology can be investigated—and, first, a great deal can be learned of the functions of the human body by careful reflection on the structure of the same. Haller[1] says: "and first the fabric of the human body is to be learned, whose parts are almost infinite. Those who would study physiology separately from anatomy certainly seem to me, can be compared with mathematicians who undertake to express, by calculation, the forces and functions of a certain machine of which they have learned neither disks, wheels, measures, nor material. Truly I am persuaded that we know scarcely anything of physiology unless we have learned it through anatomy."

Undoubtedly, the functions of many organs might be inferred from the thorough study of their structure. As a matter of history, the demonstration of the valves in the veins by Fabricius to Harvey was one of the important facts that first suggested to the latter to investigate the flow of the blood.

[1] Elementa Physiologiæ. Lausannæ, MDCCLVII. Preface, p. 1.

The functions of certain nerves will probably be never definitely settled until anatomy has determined whether they terminate in muscle, gland, or sensory organs.

Not only, however, is a knowledge of general descriptive anatomy necessary, but it is indispensable also that the student who hopes to cultivate physiology with any success, must have a thorough training in histology, or the science which has for its object the study of the tissues.

The necessity of a thorough knowledge of structure, in order to understand function, is so obvious that it seems superfluous to dwell further upon it. Pathology furnishes valuable data to the student of human physiology. Where disease is restricted to one organ, and when it is noticed that with the destruction of the tissues composing it a particular function gradually weakens and finally disappears, it is a logical inference that the loss of function is dependent upon the loss of structure. In this way the uses of many parts might be ascertained—hence, the importance of carefully kept clinical records and thorough post-mortem examination.

Suppose, for example, that, associated with loss or want of speech, in the majority of instances it is found, after death, that a particular convolution in the hemisphere of the brain is either wanting, undeveloped, or diseased—it would be a fair conclusion that the faculty of speech was connected, in some way, with this particular convolution, especially if it was clearly shown that the facts were not mere coincidence, but bore the relation of cause and effect. Or take the case of a human being suddenly paralyzed upon one side of the body both with reference to sensation and motion, and post-mortem examination revealed that certain parts of the opposite side of the brain were affected, as in apoplexy, for example. It would be natural then, to consider that the parts affected in the one side of the brain presided over the opposite side of the body and extremities—or, take the case of a man suddenly stabbed in the back-bone, the instrument penetrating only half-way through the spinal cord, and the patient loses voluntary motion on the side of the wound, and sensation on the opposite side—the view that the sensory fibers decussate in the cord, and the motor one in the medulla would be confirmed.

While, according to many thinkers, clinical medicine and morbid anatomy alone will not furnish data sufficient to deduce a physiology and a rational pathology, undoubtedly such facts as the above are invaluable as aids in throwing light upon the still obscure functions of the nervous system and the uses of other structures in the human body.

The admirable observations of Beaumont[1] and Budge[2] upon human beings, in whom the stomach and intestine had been wounded in such a manner as to render them susceptible of experi-

[1] Experiments and Observations. Plattsburg, 1833.
[2] Virchow's Archiv, Bd. xiv., s. 140.

ment, are illustrations of the application of pathological cases to the study of physiology.

When the vast complexity of structure exhibited by the human organization is considered, it becomes evident that any investigation of its function, however extended, if it be confined to man alone, can lead to but very limited results.

Comparative anatomy has shown, however, that the life of the animal kingdom is a grand panorama, each fleeting form, as it passes before the view, recalling that which has just passed, foreshadowing that which is to come; the simplest of living beings, so lowly organized and transparent that their entire life processes can be observed by the microscope, leading through intermediate forms to higher types of life, closely approaching that of man himself. With the development of additional structures, we find correspondingly increased functions, and infer that the new function is due to the new structure.

The comparative method of investigation is therefore the opposite of the pathological one, by which, as we have seen, the use of a structure is inferred from loss of function dependent upon the loss of structure.

In the hands of Harvey, Hunter, Cuvier, Muller, Milne Edwards, Owen, comparative anatomy has proved of invaluable service in the study of physiology.

In his great work, Harvey[1] states "that if anatomists had given to the organization of the inferior animals the same attention that they devote to the structure of the human body, the question of the circulation would long since have been determined."

Observations upon the enlargement of the collateral vessels in the horns of the deer when in the velvet after ligature of the carotid, suggested to the great physiological surgeon, John Hunter,[2] the idea of the collateral vessels maintaining the circulation in the thigh after ligature of the main trunk.

The ligation of the carotid in the dog,[3] and of the femoral in the same animal, done by Home[4] at the suggestion of Hunter, having further convinced the latter of the feasibility of ligation as a cure for aneurism, Hunter tied the femoral artery in the celebrated case of the coachman suffering from popliteal aneurism and thereby introduced a most capital improvement in surgery.[5]

To study the physiology of man without the slightest knowledge of life as exhibited in the lower animals is as if one would attempt to master the steam engine without any acquaintance with the elementary laws of heat or mechanics, or to investigate a magnetic apparatus without knowing anything about the simple facts of electricity.

[1] De Motu Cordis, p. 33. Frankfort, 1628.
[2] Works, edited by Palmer, vol. iii., p. 201.
[3] Ibid., vol. i., p. 444.
[4] Ibid., vol. iii., p. 597.
[5] Experimental Physiology, p. 39. Owen. London, 1882.

As the study of comparative anatomy, in its application to human physiology, at the present day, is very much neglected, it may not be superfluous to offer a few instances as illustrations of the importance of the study in this respect. For example, from the fact of the bile and pancreatic juice passing into the alimentary canal at the same point in man, it is impossible to say to which of these fluids the changes exhibited after their mixture with the food are due.

By examining the rabbit or the beaver, however, we find that the opening of the pancreatic duct into the intestine is situated twelve inches and more below that of the bile-duct. Hence, the different changes exhibited by the food as it is successively affected by these secretions, can be perfectly observed by killing a rabbit or beaver in full digestion. Indeed, as we shall see, it is in this way the emulsifying power of the pancreas is usually demonstrated.[1] Again, the question as to whether the bile is a secretion or an excretion finds its answer in the structure of the doris,[2] a little mollusk in which the liver has two ducts, one of which carries the bile into the alimentary canal, where it mixes with the food, while the other removes it at once from the body, showing that the bile, in this case at least, is both a secretion and an excretion.

One of the best established facts in physiology is that the intellectual faculties depend upon the development of the brain, both in reference to quantity and to quality. This is well seen when the brains in a series of animals are compared with reference to their intelligence. With the gradual addition of certain parts of the brain there is a corresponding increase in mental activity—and in this way, to a considerable extent, the functions of certain parts of the brain have been made out.

Embryology, or the study of the transitory phases through which every animal passes in its development from the stage of the egg to that of the adult, and which might be called the comparative anatomy of the individual, has already proved to be of service in throwing light on the functions of the human body, and which the future will, no doubt, show to be susceptible of even a wider application than is made of it at present, for the embryo of animals, with the exception of the lowest, consists of three germinal layers, of which the upper one gives rise to the epidermis and central nervous system, the lower one to the epithelium of the alimentary canal and its appendages, the middle one to bone, muscle, vessel, etc. These germinal layers, even at the start, can be readily distinguished, the cells composing them being differently affected by physical and chemical agents. Some of the lower animals, for example the hydrozoa, never get beyond this layered stage, the inner layer acting as stomach, the outer as skin. If a tissue in the adult can

[1] Bernard: Physiologie Experimentale, tome ii., p. 179. Paris, 1856.

[2] Cuvier: Memoires Pour Servir a l'Histoire et a l'Anatomie des Mollusquez. Paris, 1817. Memoire sur le Genre Doris, p. 16.

be shown to have been derived from one of these layers in its embryonic stage its function could almost be predicted. Indeed the whole modern pathological histology is an application of this view. The older pathologists, like Morgagni,[1] confined themselves to the study of the organs as affected by disease.

Bichat,[2] in investigating the tissues of which the organs are composed, created histology; Schleiden[3] first showed that vegetable tissues consist of cells, and Schwann,[4] following his lead, applied Schleiden's view to the tissues of animals. The embryologists, Reichert,[5] Kolliker,[6] Remak,[7] etc., then proved that the cells composing the tissues were the modified cells of the original mulberry mass of cells into which the egg or primitive cell segments. The obvious corollary of these generalizations followed when Virchow,[8] Billroth,[9] Paget,[10] Rindfleisch,[11] etc., showed that pathological structures were the still further modified cells composing the tissues of the organ, and that morbid growths were really physiological ones, exhibiting themselves under conditions otherwise than normal; while with the development of teratology, through the works of Geoffrey St. Hilaire,[12] and others, the explanation of the production of monsters lusus naturæ became possible. That which is pathological at one stage of growth was shown to be physiological at another; that which is normal in one animal is abnormal in another. Gradually the strict demarcation between physiology and pathology has been broken down, and, with the fusion of the two studies, a rational pathology and rational treatment are being slowly developed.

Notwithstanding the importance of a knowledge of general physics and chemistry, anatomy, embryology, and pathology in the study of the functions of the human body, nevertheless, the study of human physiology is often almost entirely based on experiments made upon living animals: the study of the circulation and respiration by means of the graphic method, the making of gastric fistulæ, the introduction into the system of an animal of various substances, toxic and narcotic, the removal of various parts of the nervous system, are examples of the kind of work often exclusively done in physiological laboratories.

The student of physiology, however, should not confine himself to the experimental methods, however invaluable and indispensable they may be as a means of investigation, but should avail himself also, as far as possible, of the other methods of research just referred to, studying the subject from all the different points of view possible

[1] De Sedibus Morborum, 1761.
[2] Anatomie Générale, 1801.
[3] Müller's Archiv, 1838.
[4] Mikroskopische Untersuchungen, 1839.
[5] Entwickelung in Wirbelthiere, 1840.
[6] Entwickelung der Cephalopoden, 1844.
[7] Entwickelung der Wirbelthiere, 1852.
[8] Cellular Pathologie, 1854.
[9] Allgemeine Pathologie, 1872.
[10] Surgical Pathology, 1870.
[11] Pathologische Anatomie, 1873.
[12] Histoire Générale et Particulière des Anomalies de l'organization, 1837.

and comparing the results obtained by the various methods made use of.

As objections are often made to the experimental study of physiology, it will not, it is hoped, be considered superfluous if we, for a moment, consider some of the most important of those usually advanced. It is often urged as an objection to a vivisection, that the pain inflicted so disturbs the normal condition that any result as to the function of a part determined in this way is valueless; the suffering entailed vitiating any conclusion as to the healthy function of the part examined. This objection is, of course, not made if anæsthetics are used. There are, however, experiments performed in which it is necessary that the animal should be in the full possession of its faculties and which, from the conditions of the investigations, make the use of anæsthetics impossible. As regards such investigations it may be said, without doubt, that animals suffer far less from the pain inflicted in a vivisection than man does from a similar wound due to an accident or the knife of the surgeon. This is due to several causes; the animal is in ignorance of what is going to be done, forgets the operation almost immediately, his nervous organization is less susceptible than that of the human being, and his wounds heal up more quickly. The influence of pain, though less in an animal than man, must nevertheless be always taken into consideration.

Whenever the vivisection is performed without an anæsthetic, the physiologist ought not to draw any conclusion from the experiment until the animal has had time to recover from the effects of the shock, hemorrhage, etc., and has so far returned to his normal condition that the influence of pain, if any still exists, is so small in amount that it cannot be considered as interfering with the function of the structure examined. It is evident, therefore, that if the physiologist had no higher motive, selfishness would induce him to be as merciful as possible and to eliminate, so far as he is able, pain, as a possible source of fallacy in his conclusions.

The animal, both during and after vivisection, should be treated just as a patient undergoing an operation would be by a wise surgeon; the object in both cases being to restore, as rapidly as possible, the physiological conditions—the conditions of health. As an illustration of what has just been said, as regards the amount of permanent disturbance produced in an animal by a vivisection, it may be mentioned that Blondlot's pointer bitch, in which a gastric fistula had been made, was used, after her recovery, by her master for eight years in the field for hunting purposes, and in the laboratory for obtaining gastric juice, and that during that period the dog had two litters of pups.

The Canadian, St. Martin, on whom the gastric fistula was caused by a gunshot wound, producing far more dangerous effects than the vivisection just referred to, lived to be eighty-four years old, enjoyed good health all his life, married and had children, per-

formed the duties of a servant, and was during this time frequently of inestimable value to science, as affording Dr. Beaumont and others the rare opportunity of observing gastric digestion in man under the most favorable circumstances.

One might as well object that the pain suffered by St. Martin, after the explosion of the gun, vitiated the conclusions drawn by Beaumont, as to object to the conclusions of Blondlot because the making of a gastric fistula in a dog involved the giving of the animal pain. A far more important objection than that just referred to is that, as animals differ very much in their organization, conclusions drawn from experiments made upon one kind of an animal cannot be applied to another kind; digestion in a dog, for example, not being exactly the same as in a man.

It is undoubtedly true that, while frogs, turtles, pigeons, rabbits, dogs, horses, etc., agree anatomically in many respects with each other and man, they disagree to such an extent that the result of experiments made upon one of these animals is often utterly inapplicable to the other, and entirely worthless as applied to man. Indeed, the most striking differences in the effect of certain substances are observed even in closely allied animals, varieties of the same species. Thus the black rhinoceros feeds upon the euphorbia, which poisons the white species; goats and lambs avoid most of the solanaceous plants; the ox and the rabbit will eat belladonna; the goat, the hemlock; the horse, aconite.

Such differences should be always taken into consideration when the results of a vivisection upon one animal are to be applied to the determination of the function of a structure in another. It must be always proved that the structure and functions compared are homologous. Further, a careful post-mortem examination should be always made after the vivisection, in order to learn exactly what has been done, to show that no structure has been involved which would modify the results except the one examined. It is the neglect of such precautions, the indifference to the infliction of pain, the comparing of utterly unlike conditions, the absence of the test of post-mortem examination, the want of controlling experiments, and of comparison of the results obtained with the facts of pathology and comparative anatomy that has brought vivisection into the disrepute in which it is held at the present day by many even educated persons. Crude generalizations, based upon imperfect experiments performed upon animals illogically applied to man, have made even medical men doubt altogether of the efficiency of this method, and account for their sympathizing with the well-meaning, no doubt, but ill-judged efforts to suppress experimental investigation altogether; and yet if vivisection should be banished from the laboratory, the physiologist would be deprived of his most fertile methods of research. The history of physiology proves not only the importance of vivisection, but its indispensability as a means of present research. Indeed, it is no exaggeration to say that there

is not an organ in the animal body whose functions have not been learned, in part at least, by vivisections. Let us illustrate this statement by a few examples.

Consider the history of the circulation of the blood, and we shall see that every important advance made in a knowledge of the subject was due to a vivisection. Thus, Galen demonstrated by vivisection that the artery contained blood and not air, as its etymology would indicate. It was by a vivisection that Harvey proved that the blood flowed from the heart to the periphery through the arteries, and from the periphery back to the heart through the veins. Finally, it was through a vivisection that Malpighi saw, for the first time, the blood actually flowing from the arteries into the veins through the intermediate vessels, the capillaries. One of the most important discoveries ever made in physiology, that of the functions of the roots of the spinal nerves, that the anterior are motor and the posterior are sensory, was demonstrated by Majendie upon a living animal. The influence of the nervous system upon the heart, so far as is known, has been entirely learned by the experimental investigations made upon animals by the Webers, Von Bezold, Ludwig, Cyon, etc. The beautiful investigations of Bernard upon the salivary glands, the pancreas, the liver, by means of vivisections, have demonstrated certain peculiarities in reference to the secretion of these organs, that could never have been learned by any other method. By means of vivisection Brown-Séquard showed the influence of the sympathetic nerve in diminishing the calibre of the blood vessels, and thence discovered the vasomotor nerves, by which the distribution of the blood to the tissues is regulated. It is needless to multiply examples of the importance of vivisection as a means of research, as nearly every chapter in this work will afford such. It must not be forgotten, however, that vivisection is but one means of physiological research, and that however important may be the results obtained by it, the latter, as already mentioned, should be always compared with such facts of comparative anatomy and pathology as have a bearing upon the function investigated, so that so far as possible all sources of fallacy may be eliminated.

To those familiar with the history of medicine any argument to prove the importance of the study of physiology would be superfluous. Physiology has always been, and is still, the cornerstone of medicine. The doctrines of Hippocrates, Galen, Sydenham, Boerhaave, Hunter, and Virchow, reflect as a mirror the physiology of the day. It is self-evident that to understand disease and its cure one must first understand health. The study of physiology must precede that of pathology and therapeutics. Hand in hand they advance together, the progress of the one depending upon that of the other. There is no better illustration of the truth of this view of the dependence of pathology and therapeutics upon physiology than ophthalmic medicine, the most developed and fin-

ished of all branches of medicine, whose present perfected condition is entirely due to the comparatively thorough understanding of the structure and function of the healthy eye.

On the other hand, diseases, like those of the nervous system, are in a proportionally backward condition owing to the imperfect knowledge of the normal anatomy and physiology of the parts involved.

Having defined the subject of physiology, considered the methods by which it is studied, and its importance to medicine, it only remains now in conclusion to indicate, generally, the order in which the study will be pursued, and here nature will be our guide. Our first sensations are those of hunger and thirst—hence the taking of food. We will, therefore, after describing the general physical and chemical structure of the body, begin with the study of digestion and absorption, the elaboration of the food into the blood, and its circulation will be then described, the consideration of excretion, animal heat, completing the study of nutrition.

But man is more than a vegetable, he feels, thinks, moves. Impressions of the outer world made upon his nervous system awaken in him consciousness, the inner world of mind. Through his nervous system man not only becomes aware of the existence of an environment, but adjusts his actions with reference to it. Finally, though the individual perishes in the reproduction of his kind, the race, temporarily at least, survives, hence the study of development. We will begin, therefore, with the study of nutrition, consider next the nervous system, concluding with an account of reproduction.

CHAPTER I.

GENERAL STRUCTURE OF THE BODY, PHYSICALLY AND CHEMICALLY.

Before taking up the study of the functions, specifically, it will be well to consider, from a general point of view, of what the human body consists, physically and chemically speaking, to obtain some general knowledge of its organization, of which the functions are the living expression.

As is known to every one, the human body, like that of a domestic animal, is made up of skin, muscles, bone; of various viscera, such as the heart, lungs, liver, stomach; of nerves, arteries, etc.

The old anatomists busied themselves almost entirely with the description of such organs, their number, size, color, relative position, etc. This kind of study may be said to have culminated in Cuvier, who, as regards the exactness, extent, and variety of his knowledge, stands without a rival as an anatomist. If, however, any one organ is examined somewhat closely, it will be found to be far from homogeneous. Thus the stomach consists of several tissues, mucous, fibrous, muscular, etc.; the heart, of muscular, connective, adipose, nervous tissue, etc. Such tissues, combined in greater or less proportions, make up the different organs of which the body is composed; the same tissue, for example, the connective, being found in different organs, just as the substance wood may be applied to making a chair, sofa, bed, or bookcase furnishing a room.

The investigation of the tissues, the creation of, histology, is due to the genius of Bichat. If now any tissue be studied in detail, it can be still further resolved into simpler ultimate physical elements or what are commonly called cells, or their modifications. This last analysis was made by Schleiden and Schwann. Through the progress of organic chemistry it has also become possible to state, with tolerable accuracy, of what the body is composed chemically. When the analysis is a proximate one, the result gives such principles as water, common salt, salts of lime; starch, sugar, fat; albumin, casein, etc. These principles exist as such in the human body, and are called proximate principles, being the result of a proximate analysis. If now these principles be analyzed, they will be found to consist of hydrogen, oxygen, sodium, chlorine, carbon, nitrogen, phosphorus, etc. In this way it is shown that the human body consists, ultimately, of the ordinary chemical elements. A human being then consists, ultimately, of myriads of cells composed of the ordinary chemical elements. Certain cells form tissues, certain tissues act together as organs, and the organs harmoniously working

together constitute a living, healthy man. The chemical elements composing the cells also act in concert, as proximate principles. A *résumé* of the above physical and chemical facts may be seen thrown together synoptically as follows :

THE HUMAN BODY CONSISTS

PHYSICALLY	CHEMICALLY
of Organs.	*of Principles.*
The organs of tissues. The tissues of cells. The cells of elements.	The principles of elements. Proximate principles.
Examples of Cells.	*of 1st Class.*
1. Cells floating in a liquid : blood corpuscles, lymph corpuscles. 2. Cells in layers : epidermis, epithelium, enamel. 3. Cells in masses : adipose tissue, medulla of hair. 4. Cells imbedded in non-cellular substance : cartilage, bone. 5. Cells forming fusiform bands : unstriated muscular fiber. 6. Cells transformed into tubes : capillaries, nerves, dentine. 7. Cells transformed into filaments: fibrous tissue, elastic tissue.	Water, sodium chloride, calcium phosphate, sodium carbonate, etc.
	of 2d Class.
	Starch, sugar, oils, fats.
	of 3d Class.
	Albumin, fibrinogen, hæmoglobin, etc.
	Ultimate Elements.
	Oxygen, hydrogen, carbon, nitrogen, chlorine, phosphorus, sulphur, calcium, sodium, potassium, magnesium, iron, fluorine, iodine, silicon.
A cell may consist, in its wall, of membrane ; in its contents, of liquid and granules ; in its appendages, of filaments.	

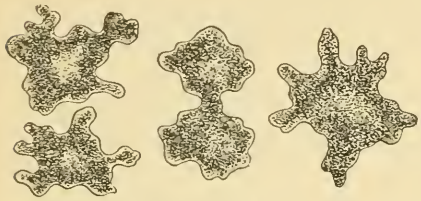
Let us now take up somewhat more in detail what is known of cells and proximate principles. A cell may be defined as the ultimate elementary living unit, a mass of living matter, varying from the $\frac{1}{2000}$ mm. to $\frac{1}{5}$ mm. ($\frac{1}{5000}$th to the $\frac{1}{120}$th of an inch) in diameter. It may consist of a cell wall, inclosing cell contents of a liquid, semi-liquid, or granular character. The granules in some cells are united, according to many histologists, by filaments or threads ; the cell contents consisting then of a network. Often among the cell contents can be distinguished a still smaller cell, the nucleus, and, within this, the nucleolus. Sometimes the cell wall is elongated into an appendage, a cilia. Great difference still prevails among histologists, etc., as to the relative importance of the nucleus and nucleolus of the cell contents and cell wall.

According to some observers, the all important element in cell life is the nucleus, while others maintain that it is the cell contents. The cell wall and even the nucleus are regarded by some as the cell contents in a state of retrograde metamorphosis.

As we proceed in our studies, it will be seen that there are cells,

like the blood corpuscles, which have neither nucleus nor cell wall; Further, there are protoplasmic beings, like the monera, of which the protamœba (Fig. 1) is an example which, through life, never exhibit either nucleus or cell wall. Such facts prove that in certain cases at least, neither the nucleus nor cell wall is an indispensable element to the life of cells, and should make physiologists cautious in attributing positive functions to this or that element of a cell. Indeed, it cannot be said that the

Fig. 1.



Protamœba. (Heckel.)

relative significance of either nucleus, nucleolus, cell wall, or cell contents, is as yet definitely understood. As examples of cells, attention may be called to those lining the uriniferous tubules of the kidney, to the cells of the enamel, to those of the epithelium of the mouth (Fig. 2), of the columnar epithelium of the intestine, to the multipolar cell found in nervous tissues, to the ciliated epithelial cells from the pulmonary mucous membrane (Fig. 3), to blood

Fig. 2.

Buccal and glandular epithelium, with granular matter and oil-globules; deposited as sediment from human saliva. (Dalton.)

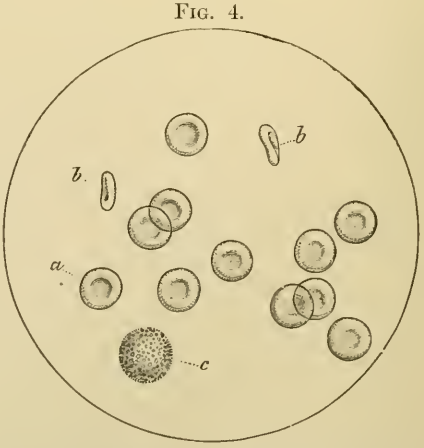
Fig. 3.

Columnar ciliated epithelium cells from the human nasal membrane; magnified 300 diameters. (Quain and Sharpey.)

cells (Fig. 4), to unstriated muscular fiber cells.

As we take up the different organs, the cells composing their tissues will be described more in detail;

Fig. 4.



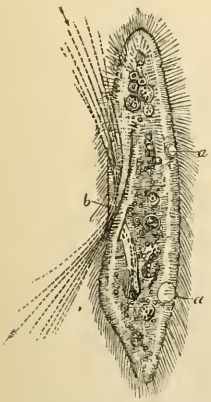
Human blood-globules. *a*. Red globules, seen flatwise. *b*. Red globules, seen edgewise. *c*. White globule. (Dalton.)

so the above examples will, therefore, suffice for the present in giving a general idea of the form of cells.

While there is still some doubt as to the exact use of the different parts of the cells, there is no doubt that the life of the organism resides in the cells composing it. Among other reasons for supposing so, may be mentioned the fact that the life of the human being begins as the ovum, a cell, and that the tissues of the embryo, out of which are built up the organs of the adult, consist of modified cells, the lineal descendants of this primitive cell or ovum, and inheriting its life characteristics, the life of the organism being the resultant of the lives of the individual cells composing it.

The independent life of cells is well seen in some of the lower animals, whose blood corpuscles can be observed actually feeding upon substances artificially introduced into the circulation, and in the embryonic state can be observed dividing and subdividing, and so reproducing themselves. Gland cells, like those of the liver, kidney, etc., in taking from the blood the materials out of which their respective secretions are elaborated, show their independent activities. Pathological processes often present chances for observing this independent cell life, in the wandering of the white and red blood cells out of the vessels, in the rapid proliferation of cells seen in the development of various morbid growths, etc. The protozoa and protophyta, or the simplest of animals and plants, however, offer the most favorable opportunities for observing the life history of cells; for these simple beings never get beyond the one-cell stage of life, indeed neither tissues nor organs are ever developed in them in the same sense that these are in the higher animals. The entire life cycle of these minute plants and animals can be often followed under the microscope. The manner in which cells take food, move about, their mode of reproduction—usually through simple division, though sometimes endogenously and by gemmation and conjugation—can be readily observed by an examination of the greenish matter on damp bricks, stones, etc., consisting usually of palmoglea, micrococcus, or the greenish film-like spirogyra seen covering the ditches and ponds in the neighborhood of the city, and which also usually contain specimens of unicellular protozoa paramœcium (Fig. 5), stentor, as well as desmidiaceæ, of which Fig. 6 is an example. These researches, always interesting to the mere microscopist on account of the beauty of the vegetable and activity of the animal forms, have a deep meaning to the philosophical physiologist. For it is reasonable to suppose that the life of man or the higher animals, when in the one-cell or ovum stage (Fig. 7), is similar to that of these beings

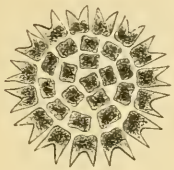
Fig. 5.



Paramœcium caudatum. *a, a.* Contractile vesicles. *b.* Mouth. (Carpenter.)

which pass beyond this unicellular stage. Hence, we may conclude that the human ovum, or any of the cells descended from it, absorbs and assimilates nutriment, like the unicellular beings just referred to. The segmentation of the egg in the higher animals corresponds also to the division of the cell seen in the reproduction

FIG. 6.



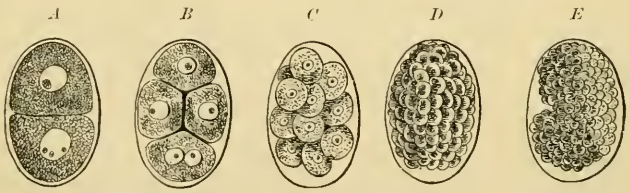
Pediastrum pertusum. (CARPENTER.)

FIG. 7.

Human ovum, magnified 85 diam. *a*. Vitelline membrane *b*. Vitellus. *c*. Germinative vesicle. *d*. Germinative spot. (DALTON.)

of these minute beings, the manner in which the nucleus divides first into two halves and the cell contents or protoplasm constricts around the new nuclei being essentially the same in both cases; the only difference being, as we shall see hereafter, that in the former

FIG. 8.



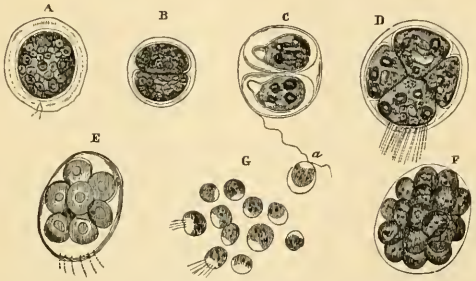
Division of the yolk of Ascaris. A, B, C (from Kölliker), ovum of Ascaris nigrovenosa; D and E, that of Ascaris acuminata (from Bagge). (QUAIN and SHARPEY.)

the new cells hold together and are transformed into tissue, in the latter the new cells are scattered, constituting the next generation of cells. This distinction may be seen by comparing the segmentation of ascaris (Fig. 8) with the reproduction of protococcus through continued subdivision (Fig. 9). In either case, however, the life of the resultant cells is that inherited by them from the parent cell. The cells resulting from the segmentation of the mammalian ovum or egg are at first very similar, but soon a marked difference between them can be observed. According to the researches of Van Beneden on the rabbit, the difference is noticeable even in the two first segmentation cells. However this may be, the cells soon begin to differ in size, shape, and the manner in which they are affected by chemical agents. Some dispose themselves so as to form the epi-

blast, others the hypoblast, and between these two layers a third appears, the mesoblast.

The modification of the cells and the further development of these three layers will be considered when we take up the subject of reproduction. It will be seen then that through the processes incidental to development, cells often lose their originally round form, becoming sometimes flattened or scale-like, and often of a prismatic and columnar shape. Sometimes the cells float free in a liquid, like the blood corpuscles; or they may arrange themselves in layers, like those of the enamel; or in masses, as seen in the medulla of hairs. They may be imbedded in a solid non-cellular matrix, as in cartilage. Cells are sometimes flattened into bands, as in the unstriated

FIG. 9.



Development of Protococcus pluvialis. (CARPENTER.)

muscular fiber, or a number are, through the dissolution of their adjacent walls, metamorphosed into tubes, of which the capillaries and dentine are examples, or they may be converted into fibrous tissue. These modifications are shown synoptically arranged in the table giving the physical constituents of the body. The various substances elaborated by cells in different parts of the adult economy will be more appropriately considered as the functions of the organs are taken up. It will be seen that the life of the body is, therefore, the resultant life of the cells composing it; that the body is a living republic of cells.

Let us now return to the chemical composition of the body, or of the cells of which it consists. We have seen that the human body consists of chemical elements acting as proximate principles.

A proximate principle may be defined as a principle, simple or compound, which exists and acts as such in the human body. Thus, sodium chloride is a proximate principle. Neither the rare metal sodium, nor the offensive greenish gas chlorine, however, are proximate principles, for they do not exist or act as such in the body. Calcium phosphate is an example of a proximate principle; but the metal calcium, and the phosphoric acid, not existing or acting separately, as calcium and phosphoric acid, in the body, cannot

be regarded as proximate principles. The purely analytical chemist would resolve such proximate principles as fat, albumin, into their ultimate elements, carbon, hydrogen, oxygen, nitrogen, and sulphur respectively. The physiological chemist, however, would study these principles without further decomposition, investigating the part that fat and albumin play as such in the economy without regard to their ultimate chemical composition.

Proximate Principles.

Leaving out of consideration for the present the gases, which can be more conveniently treated of under the subject of the blood, the proximate principles can be divided, for convenience of description, into those of inorganic and organic origin, the latter being further subdivided into those in which nitrogen is absent and those in which it is present.

PROXIMATE PRINCIPLES OF THE FIRST CLASS, OR THOSE OF INORGANIC ORIGIN.

Substances.	Where found.
Water	Universal.
Sodium chloride	Universal, except enamel.
Sodium sulphate	Universal, except milk.
Sodium phosphate	Universal.
Sodium carbonate	Blood, saliva, lymph.
Potassium chloride	Muscles, blood, saliva, gastric juice.
Potassium phosphate	Universal.
Potassium sulphate	Bile, gastric juice.
Potassium carbonate	Bones, lymph.
Calcium chloride	Bones.
Calcium fluoride	Bones, dentine, enamel.
Calcium sulphate	Blood, feces.
Calcium phosphate	Universal.
Calcium carbonate	Bones, teeth, cartilage.
Magnesium phosphate	Blood, bone, muscle.
Iron	Blood, bile, feces.
Silicic acid	Hair, urine.
Iodine	Thyroid body.

As implied in the definition, the principles of this class are inorganic in origin, being found in the rocks forming the crust of the earth, in sea water, springs, etc., and are crystallizable. With the exception of calcium carbonate, of which the otoliths of the ear consist, they are combined in the body with the organic principles. This union is so intimate that as the organic principles become effete, and are eliminated, the inorganic substances are cast out with them. Some of these substances play a more important *rôle* than others, and are found in greater or less quantities in the economy.

Let us consider now the most important of these substances, where they occur, and their principal uses.

Water, H_2O.—In the maintenance of life, none of the proximate principles, whether inorganic or organic, surpass in importance

water. When it is learned, however, that it constitutes nearly 68 per cent. by weight of the whole body, this will no longer be a subject of surprise. In the course of our studies we shall find that water exists in all parts of the body: in solids, like bone and enamel; in fluids, like the tears, perspiration, etc. Its uses in the economy are manifold. It gives consistence and general resiliency to the body, pliability to tendons, elasticity to cartilage, resistance to the bones. Various substances, like articles of food and the effete matters, find their way into and out of the body through their solubility in water. The importance of water is at once seen if the system is deprived of it. The tissues become shrivelled and dried up and inflexible, the liquids become thick, inspissated, lose their fluidity. On the other hand, an excess of water gives rise to general debility, muscular weakness, dropsies, etc.

In the living body water exists as "water of composition"—that is, it constitutes an integral part of the tissues. The water is not taken up by the tissues, like a sponge, but really forms a part of its substance, the union being a chemical one.

QUANTITY OF WATER.[1]

Substance.	Parts per 1000.	Substance.	Parts per 1000.
Enamel	2	Milk	887
Epithelium	37	Chyle	904
Teeth	100	Bile	905
Bones	130	Urine	933
Tendons	500	Lymph	960
Cartilages	550	Saliva	983
Skin	575	Gastric juice	984
Liver	618	Perspiration	986
Muscles	725	Tears	990
Ligaments	768	Pulmonary vapor	997
Blood	780		

The relative amount of water, in the tissues, is regulated by the salts. Thus, when water is added to the blood, the corpuscles become swollen, and finally are dissolved away; but if a strong solution of salt be added instead, the corpuscles lose their water and shrivel up. Most of the water found in the system is taken in as part of the solid and fluid articles of the food. As we shall see hereafter, however, about 300 grammes (4629 grains) are formed in the system through combustion of hydrogen.[2] The daily amount of water necessary for the healthy adult is estimated, by Dalton,[3] at about 2 kil. (4.4 lbs.). This, of course, includes the water entering into the solid articles of food. About fifty-two per cent. of the water, after it has played its part in the economy, is discharged by the skin and lungs, the rest by the kidneys and with the feces. When, however, the skin is not active, as in the winter

[1] Robin et Verdeil, op. cit., p. 115.
[2] Dalton, Physiology, 1882, p. 37.
[3] Op. cit., p. 36.

time, then the kidneys act very freely; in the summer the reverse is the case. Diuretics favor the one set of emunctories, diaphoretics the other.

By glancing at the Table it may be seen how universally water is found in the tissues, and its relative amount. Thus, while we find that a thousand parts of pulmonary vapor contain nine hundred and ninety-seven parts of water, it will be seen there are only two parts of water in a thousand of enamel, and that a substance, like tendon, so different from either of those just mentioned, is half made up of water. The great importance of water in health, and still more in disease, cannot be too much dwelt upon by the physiologist and practising physician.

Salts of Sodium.

Sodium Chloride, NaCl.—Next to water, common salt is the most important of the inorganic proximate principles, being found, like water, almost universally, even in the ovum. With the exception of the enamel, in which it has not yet been discovered, salt is found in all the solids and fluids of the body. The absolute amount, however, has not yet been determined. The saltish taste of the tears and perspiration is due to the presence of this principle. It is found in the largest proportion in fluids.

QUANTITY OF SODIUM CHLORIDE.[1]

Substance.	Parts per 1000.	Substance.	Parts per 1000.
Blood	6.04	Saliva	1.5
Chyle	5.3	Perspiration	3.4
Lymph	4.1	Urine	4.4
Milk	0.8	Feces	3.0

Salt is introduced into the system through the different articles of animal and vegetable food which always contain it; in addition, salt as such is added to the food of man and the herbivora; the amount contained in their food not being sufficient for the wants of the economy. Salt, like all other inorganic principles, passes ultimately through the body, and is carried out of it in the urine, feces, perspiration, etc.

Recent experiments[2] have shown that the excretion of sodium chloride does not depend simply on the amount ingested, since in some cases the sodium chloride excreted was much greater for several days than that taken as food, the excess being supplied by the tissues.

The uses of salt in the system are manifold. Disintegration of the red blood corpuscles is prevented through the presence of salt. A solution of sodium chloride having a strength of 0.6 per

[1] Robin et Verdeil, op. cit., p. 76.

[2] Klein und Verron, Sitzungsberichte der Wiener Academie Math.-Phys. Klasse, 1867, s. 627.

cent., the amount in which it is present in the blood, is often called the "physiological salt solution" and is said to be "isotonic" to the red corpuscles since the latter retain their form and coloring matter in the same. The phenomena of osmosis, or the passage of fluids and gases through animal membranes, are greatly modified by the amount of salt present, a solution of salt osmosing through a membrane much less readily than pure water. Absorption is influenced by it. It increases the solubility of albumin; this substance being less quickly coagulated by heat in a solution of sodium chloride than in water. From sodium chloride is derived the hydrochloric acid of the gastric juice. Salt is of great use as a condiment, it being impossible to support life on food without flavor, however good the latter may be in quantity or quality. Nutrition is undoubtedly affected in other ways by salt, as yet not perfectly understood. The experiments of Boussingault[1] upon bullocks, and of Dailly[2] upon sheep, showed what a deleterious effect was produced in their general appearance when these animals were deprived of salt. It is well known how the wild buffalo is found by the salt licks of the Northwest, and how the hunter in Southern Africa avails himself of his knowledge of the habits of wild animals collecting near salt springs, to kill his game. Every one is familiar with the fact of how cattle run to any one who will give them salt. It is said that fugitives from justice will often risk capture and their lives to obtain salt. Facts like the above show what a deep-seated want is felt by man and beast alike when deprived of salt.

Sodium Sulphate (Na_2SO_4), commonly called Glauber salts, is found in the blood and other fluids of the body. It is introduced into the system with food and discharged together with potassium sulphate in the urine in the condition which we shall see hereafter is known as "preformed sulphuric acid." The diarrhœa that sulphate of sodium gives rise to when administered in purgative doses is probably due to the epithelial cells of the intestine being affected in such a manner by this, as by other laxatives, as to prevent the absorption of water. Sodium phosphate exists in the fluids of the economy, the blood for example, both as monosodium phosphate (NaH_2PO_4) and disodium phosphate (Na_2HPO_4). These salts are taken into the body as food and are discharged in the feces and urine. The acidity of the urine, as will be shown when that excretion is considered, is principally due to the monosodium or primary acid phosphate (NaH_2PO_4). The latter osmoses or passes through membranes more readily than the disodium or secondary sodium phosphate. Sodium carbonate ($NaCO_3$) is found in the blood, lymph, saliva, pancreatic, intestinal juices, etc. It is produced within the body by the oxidation of organic sodium salts, or is introduced with the food. To the existence of this salt the alkalinity

[1] Chimie Agricole, p. 271. Paris, 1854.
[2] Longet: Traité de Physiologie, tome i., p. 76.

of the economy is principally due. Its importance may be appreciated from the fact that carbon dioxide will not pass from the tissues in acidified blood and that death can be prevented in an animal, whose blood has been acidified by feeding with acid, by venous injection of sodium carbonate. Through reaction with the carbon dioxide given by the tissues to the blood the sodium carbonate, in presence of water, becomes sodium bicarbonate or acid carbonate ($NaHCO_2$).

$$Na_2CO_3 + CO_2 + H_2O = NaHCO_3 + NaHCO_3$$

Through the further action of acids both carbonates give up their carbon dioxide. The carbon dioxide set free is usually regarded as being of advantage mechanically to the economy, the particles of the chyme, for example, being separated by it and rendered more susceptible to the action of the intestinal juice in the same manner as we shall see the digestion of food by gastric juice is promoted by previous admixture with saliva.

Salts of Potassium.

Potassium Chloride, KCl.—This principle is found in the muscles, blood, saliva, bile, gastric juice, urine, etc. A greater part of it is introduced into the system with the food, though probably some is produced through the double decomposition of the potassium phosphate and sodium chloride existing in the blood, sodium phosphate and potassium chloride resulting.

$$KH_2PO_4 + NaCl = NaH_2PO_4 + KCl$$

The uses of potassium chloride and sodium chloride are probably the same in the economy. This principle is discharged from the body in the mucus and the urine.

Potassium phosphate is found in small quantities in the solids and fluids of the body, generally existing both in the form of monopotassium phosphate (KH_2PO_4) and the dipotassium phosphate (K_2HPO_4). The potassium phosphates are introduced into the body with the food and are discharged in the feces and urine. Their function in the economy appears to be associated with the activity of protoplasm in general, they constituting the principal salts of the cells of the body. The monopotassium phosphate or the so-called primary phosphate contributes to the acidity of the urine, and is also the cause of the acidity exhibited by muscle during the condition known as rigor mortis.

Potassium Sulphate (K_2SO_4) exists in small quantities in the blood, etc. It is introduced into the body in the food, and discharged in the feces and urine.

Potassium Carbonate is found in small quantities in the blood, lymph, and other parts of the body, both in the form of acid carbonate ($KHCO_3$) and of neutral carbonate (K_2CO_3). These salts are introduced to a great extent into the economy with food, and

when excreted in the urine in sufficient quantity render it alkaline. The acid carbonate appears to be produced within the body, especially in the blood corpuscles and the plasma, through the action of carbon dioxide and water upon dipotassium phosphate, the latter being transformed at the same time into the monopotassium salt as follows:

$$K_2HPO_4 + CO_2 + H_2O = KHCO_3 + KH_2PO_4$$

The neutral carbonate may also be produced within the body through the oxidation of an organic salt of potassium, such as the tartrate

$$K_2C_4H_4O_6 + 5{,}O = K_2CO_3 + 3CO_2 + H_2O$$

Experiments made in the laboratory render it highly probable that potassium carbonate and sodium chloride react upon each other in the body, the double decomposition supposed to take place giving rise respectively to sodium carbonate and potassium chloride ($K_2CO_3 + 2NaCl = 2KCl + Na_2CO_3$). Inasmuch as both these substances are excreted in the urine, it is evident that food rich in potassium salts, like potatoes when eaten, entail a loss of sodium chloride to the economy. Hence the necessity, in order to make good this loss, of adding salt to the food, when the latter is largely of a vegetable character. On the other hand, if the diet consists principally of rice, relatively poor in potassium salts, the use of salt can be, to a great extent, dispensed with. Salt is not used, as a general rule, in cases where the food consists solely of fish and meat, the blood of the animals eaten supplying the sodium salts.[1]

Salts of Calcium.

Calcium chloride ($CaCl_2$) occurs in small quantities in bones and calcium fluoride ($CaFl_2$) in bone, dentine and enamel. Difference of opinion still prevails among chemists as to the manner in which the mineral substances of bone are combined with each other. Chlorine and fluorine appear to be present[2] in the same form as in the mineral apatite ($CaFl_2$, $3Ca_3P_2O_8$). Calcium sulphate ($CaSO_4$) is also found in bone in small quantities. It is often introduced into the economy through the use of spring and well water in which it is present. It is discharged from the body in the feces, being occasionally found in the sediment of strongly acid urine.

Tricalcium Phosphate, $Ca_3P_2O_8$.—This very important substance is found in all the solids and fluids of the body. It will be seen, however, that calcium phosphate exists in much larger proportions in the solids than in the fluids. Only traces are found in blood, saliva, etc., whereas a thousand parts of enamel will contain nearly nine hundred parts of this principle.

[1] Bunge, Lehrbuch der Physiologischen und Pathologischen Chemie, Dritte Auf., 1894, s. 108–116.

[2] Olof Hammarsten: A Text Book of Physiological Chemistry. Translated by John A. Mandel, 1893, p. 238.

QUANTITY OF CALCIUM PHOSPHATE.[1]

Substance.	Parts per 1000.	Substance.	Parts per 1000.
Blood	0.7	Teeth of infant	510.0
Milk	2.5	Teeth of adult	610.0
Saliva	0.6	Teeth of man at 81 years	660.0
Urine	25.0	Enamel	885.0
Excrements	40.0	Rachitic bone	136.0
Bone	400.0		

Calcium phosphate is introduced into the system in the food and is eliminated in the urine and feces, being continuously excreted into the intestinal canal.

Calcium phosphate, although insoluble in water, is held in solution in blood, milk, etc. In the case of blood it is difficult to explain this unless the salt is in combination with the proteids of the blood as it is with the casein of milk, and with the protoplasm of the cell.

Calcium phosphate is found in a sedimentary condition in the urine, but only after the latter becomes alkaline. Under these circumstances it is derived from the acid phosphates, calcium phosphate occurring in the urine as primary ($CaH_4(PO_4)_2$) and secondary ($CaHPO_4$) phosphates.

Calcium phosphate exists in a solid condition, bones, teeth, cartilage, etc. The calcium phosphate in a bone can be all dissolved out by hydrochloric acid; such a bone retains its form, but if it be the fibula, is so pliable that it can be tied in a knot, a good illustration of the importance of this salt to the system. On the other hand, after complete calcination of bone which destroys its organic substance, the ossein, there remains the so-called bone earth, consisting of calcium and phosphoric acid. The use of calcium phosphate in the economy is to give strength and solidity. Hence the large amount present in the bones, and more especially in the enamel, the hardest of all known organic substances. It is very abundant in the lower extremities, which support the weight of the body. The ribs contain less calcium phosphate than the upper extremities, hence their greater elasticity.

The amount of calcium phosphate found in any organ or tissue differs often according to age; thus it will be observed that in the teeth of a very old man, in a thousand parts there are one hundred and fifty parts more than in an infant, and fifty more than in an adult. The liability of pregnant women to meet with fractures, and the delay of union in these cases, are due to their offspring taking from the mother so much calcium phosphate, essential to the development of the new being.

In recent years it has been shown that the salts of calcium play an important part in the phenomena of coagulation. Indeed, in their absence, as we shall see, blood will not coagulate. If animals be deprived of their proper amount of calcium salts their bones

[1] Robin et Verdeil, op. cit., p. 287.

will soften, as shown by the experiments of Chossat,[1] Voit,[2] and Weeske.[3] Rickets is generally held to be due to a deficiency in the calcium salts of the food. Recent experiments[4] show, however, that rickets will persist in children, even when the food contains the normal quantity of this salt. The disease may be due, therefore, not so much to a deficiency of calcium phosphate as to some want of assimilation.

Neutral Calcium Carbonate, $CaCO_3$.—This principle is found in the blood, teeth, cartilage, and bones. In the latter it is not as abundant as the phosphate, but exists in the proportion of a hundred parts to the thousand.

QUANTITY OF CALCIUM CARBONATE.[5]

Substance.	Parts per 1000.
Bone	102.0
Teeth of infant	140.0
Teeth of adult	100.0
Teeth of man at eighty-one years	10.0

As before mentioned, calcium carbonate is the only inorganic principle which exists in a crystalline form and uncombined in the body. As such, it is found in the otoliths of the internal ear. Calcium carbonate appears to exist in bone in the form of apatite ($CaFl_2 3(Ca_3P_2O_8)$), the CO_3 occupying, however, in bone ($CaCO_3 3(Ca_3P_2O_8)$) the position of Fl_2 in the mineral.

Calcium carbonate is found in the food, and is introduced in this form into the system. It passes out of the body in the urine, probably transformed into the phosphate. The uses of calcium carbonate in the economy are essentially the same as those of calcium phosphate.

Neutral calcium carbonate, although insoluble in water alone, becomes soluble in the presence of water and carbon dioxide, being transformed, however, through the reaction into the acid carbonate, $CaCO_3 + H_2O. + CO_2 = CaH_2(CO_3)_2$. In the latter form as a soluble acid salt, calcium carbonate occurs in the blood, lymph, pancreatic juice and in small quantities in the tissues generally. The calcium carbonate of the saliva, together with bacteria and organic matter constitute the so-called tartar of the teeth.

Salts of Magnesium.

Magnesium, wherever present, is always associated with calcium as tertiary magnesium phosphate ($Mg_2(PO_4)_3$). It is found in the blood, muscle, and bone, constituting one per cent. of the ash of the latter. Magnesium phosphate is introduced into the system with

[1] Recherches experimentales sur l' Inanation, 1843, p. 28.
[2] Hermann, Handbuch, 1881, Band vi., 1, s. 379.
[3] Zeitschrift für Biologie, 1894, Band 31, s. 421.
[4] Rudel, Archiv für experimental Pathologie und Pharmakologie, 1893, Band 33, s. 90.
[5] Robin et Verdeil, op. cit., p. 223.

the food and, being excreted by the walls of the alimentary canal and kidneys, passes out of the body in the feces and urine, occurring in the latter as primary and secondary phosphate. During the ammoniacal fermentation of the urine magnesium is precipitated as ammonium magnesium phosphate ($MgNH_4PO_4$).

The importance of this salt as well as that of ammonium sodium phosphate and of ammonium carbonate will be considered hereafter.

Iron.

Iron is found either in combination with other chemical elements or with organic substances throughout the economy. As ferric phosphate ($FePO_4$) it occurs in the gastric juice, bile. In the form of ferrous sulphide (FeS) it is found in the feces. In the liver and spleen it exists as ferratin and hepatin, and in the urine also as an organic compound. It enters into the composition of hæmoglobin, and, as we shall see, is one of its most important ingredients. According to recent observations [1] it is only organic iron, such as found in the yolk of eggs as hæmatogen, and in plants in the form of nucleo-albumins containing iron, that is absorbed by the system, inorganic iron being unabsorbable. Ferric chloride is, however, of benefit to the economy when administered internally, since, being converted into ferrous sulphide by the action of sulphuretted hydrogen,

$$Fe_2Cl_6 + 2H_2S = 2FeS + 4HCl + Cl_2$$

the organic iron of the system amounting to about 4 grammes (61.7 grains) may be protected from a similar transformation with subsequent elimination. The importance of iron to the economy is shown by the fact that when deficient in the food the organic iron of the system is drawn upon to make good the deficiency. Thus for example [2] in the case of a dog in which the iron in the food amounted to 0.93 grammes (14.34 grains) that of the feces for the corresponding period was as much as 3.59 grammes (55.39 grains), the difference, 2.66 grammes (41.05 grains), being supplied at the expense of the organic iron of the body.

Silicon.—This substance occurs as silicic acid (H_4SiO_4) in hair and the urine. It is introduced into the economy in the food, being found in the yolk of eggs, and vegetables.

Iodine is found as thyroiodin in the thyroid gland.

[1] Bunge, Zeitschrift für physiologische Chemie, 1885, Band 9, s. 49. Marfori, Archiv für exper. Pathologie und Pharmakologie, 1892, Band 29, s. 212. Schmiedeberg, Archiv für exper. Pathologie und Pharmakologie, 1894, Band 33, s. 101.

[2] Voit, Hermann, Handbuch, Band vi., Erstei Theil, s. 385.

CHAPTER II.

PROXIMATE PRINCIPLES OF ORGANIC ORIGIN.

As has been already stated, in addition to the inorganic proximate principles the human body contains many of organic origin, that is of principles elaborated by organized bodies, plants, and animals. It is well known, however, that many of these principles have been prepared in the laboratory from inorganic elements by chemists without invoking the aid of a so-called "vital force" and there is every reason to suppose that in time they will all be. Such being the case the distinction between bodies of inorganic and organic origin regarded at one time as so essential is without philosophical significance, and is only made use of in this connection as a matter of convenience.

Principles of Organic Origin.

PROXIMATE PRINCIPLES OF THE SECOND CLASS.
NITROGEN ABSENT.

Substances.	Where found.
Sugar	Milk.
Starch	Brain.
Lactic acid	Small intestine
Oxalic acid	Urine.
Inosite	Muscles.
Fat	Almost universally.

PROXIMATE PRINCIPLES OF THE THIRD CLASS.
NITROGEN PRESENT.

Substances.	Where found.
Serum albumin	Blood.
Fibrinogen	Blood.
Hæmoglobin	Blood corpuscles.
Mucin	Mucus.
Casein	Milk.
Keratin	Nails.
Sodium taurocholate	Bile.
Cystein	Urine.
Lecithin	Nervous system.
Xanthin	Urine.
Indol	Feces.
Pepsin	Gastric juice.

These principles, as shown by the table, may be divided, for convenience of description, into two classes: one in which nitrogen is absent, the proximate principles of the second class, and one in

which that element is present, the proximate principles of the third class.[1] The former will be first considered.

Proximate Principles of the Second Class, or non-Nitrogenous Principles of Organic Origin.—These principles include the sugars, starch, fats. They do not enter into the constitution of the mineral world like sodium chloride, calcium phosphate, etc., just considered, being ordinarily produced, at least by plants and animals. In striking contrast also with the principles of the first class, those of the second class, with the exception of the butter and sugar of milk, are never discharged as such from the body in a state of health. Sugar in the urine, for example, is a symptom of diabetes; fat in the feces, of disease of the pancreas. The principles of the second class, with the exception of starch, are, however, crystallizable, agreeing in this respect with those of the first class.

Composition of	
Water	H_2O
Grape sugar	$C_6H_{12}O_6$
Cane sugar	$C_{12}H_{22}O_{11}$
Starch	$C_{18}H_{30}O_{15}$
Lactic acid	$C_3H_6O_3$
Inosite	$C_6H_{12}O_6$
Stearin (fat)	$C_{57}H_{110}O_6$

It will be observed that sugar, starch, lactic acid, and inosite differ from fat in that the hydrogen present in the former substances just suffices, with the oxygen, to form water, whereas in neutral fats the hydrogen is in excess. It might naturally be supposed that the former substances would form a natural group and the fats another. Chemically speaking, however, the sugars and starch are regarded as constituting one group, carbohydrates; lactic acid as an oxy-fatty acid, and inosite as a member of the aromatic series. Let us begin our study of these principles with the carbohydrates.

A carbohydrate is a substance which consists of carbon, hydrogen, and oxygen, the atoms of carbon varying in number, the atoms of hydrogen and oxygen in the proportion to form water. The carbohydrates are divided into three distinct groups: glycoses, disaccharides, polysaccharides, of which grape sugar, cane sugar, and starch are respectively familiar examples. Glycoses include such substances as glycerose, made up of the tryoses, glycerin aldehyde, and dioxyacetone, erythrose ($C_4H_{10}O_4$), as well as the monosaccharides, glucose,

[1] It is to be understood that the above division, however useful for purposes of description, is an artificial one, not based upon chemical relationship, since nitrogenous substances occur in the body, which may be derived from non-nitrogenous ones, and *vice versa*. Thus, for example, as we shall see hereafter, Urea, a nitrogenous substance, regarded as carbamide, is carbon dioxide, in which one atom of oxygen is replaced by the residue of two molecules of ammonia. On the other hand, bodies, like fats, non-nitrogenous substances, may be derived from proteid nitrogenized ones.

galactose, and levulose. The latter, while consisting chemically of $C_6H_{12}O_6$, differ from each other in their atomic arrangement. It will be observed that in the glycoses the number of carbon atoms is the same as that of the oxygen atoms. It may be appropriately mentioned, also, in this connection, that, according to the number of carbon atoms present in a glycose, the latter is called a triose (glycerose), tetrose, hexose (monosaccharides), nonose. Glucose and galactose are usually regarded as being the aldoses of the hexatomic alcohols, sorbite and dulcite, respectively; that is, as having the constitution of an aldehyde alcohol (CH(OH)CHO). Aldehyde is alcohol[1] dehydrogenated and is produced by the action of oxygen upon alcohol

$$\underset{\text{Alcohol.}}{C_2H_6O} + \underset{\text{Oxygen.}}{O} = \underset{\text{Aldehyde.}}{C_2H_4O} + \underset{\text{Water.}}{H_2O}$$

Galactose is found in the brain, combined with proteid in the form of the glucoside[2] cerebrin. It is produced in the economy through the hydrolytic decomposition of milk sugar, glucose being produced at the same time. Levulose, d-fructose, fruit sugar, found in fruits and honey, is produced in the body through the decomposition of cane sugar and is transformed into glucose. Levulose, being the ketose of mannite, is therefore a ketone alcohol[3] ($COCH_2OH$).

The disaccharides, cane sugar, milk sugar, and maltose are, as their name implies, dimultiple sugars, each consisting of $C_{12}H_{22}O_{11}$, but differing in their atomic arrangement. Saccharose cane sugar is obtained from the cane beet root. We shall see hereafter that cane sugar is converted or inverted into glucose and levulose by the hydrochloric acid of the gastric juice and intestinal ferment. On this account cane sugar, when eaten, becomes indirectly a source of glycogen.

Dextrose, d-glucose, or grape sugar ($C_6H_{12}O_6$), is found in the blood and tissues of the body to an extent of about 0.5 per cent. It is derived, as we shall see hereafter, from the digestion of starch, cane sugar, the decomposition of proteid, the dehydration of glycogen. A convenient and delicate test for grape sugar is the well-known one of Trommer. It is made in the following manner: The suspected liquid is placed in a test-tube; to this are added one or two drops of sulphate of copper; then the mixture is made distinctly alkaline by the addition of a solu-

[1] Aldehyde (CH_3CHO) being alcohol (C_2H_5OH) dehydrogenated, an aldehyde alcohol is a substance containing the groups CHO and OH, characteristic of aldehydes and alcohol respectively.

[2] A glucoside is a substance which, in the presence of water and a ferment, yields glucose, etc. Thus for example,

$$\underset{\text{Amygdalin.}}{C_{20}H_{27}NO_{11}} + \underset{\text{Water.}}{2(H_2O)} = \underset{\text{Benzoic aldehyde.}}{C_7H_6O} + \underset{\text{Hydrocyanic acid.}}{CHN} + \underset{\text{Glucose.}}{2C_6H_{12}O_6}$$

[3] A ketone, as, for example, acetone (CH_3COCH_3), being characterized by containing the group CO, a ketone alcohol is a substance containing the groups CO and OH, characteristic of a ketone and alcohol.

tion of caustic potash. The mixture will become blue, particularly if sugar is present. Now heat the test-tube till just before boiling point, when, if sugar is present, a reddish precipitate will appear just in the upper part of the tube, and will gradually be seen in the whole liquid. The reaction is due to the cupric oxide being reduced to the condition of a cuprous oxide by the oxidation of the sugar. The solution to be examined should be clear. This can be accomplished by boiling the suspected tissue, finely divided, with water and sulphate of soda and filtering. The organic and coloring matters will be retained, and a clear extract will pass through, the soda not interfering with the test. Maltose and lactose respond to Trommer's test. Cane, maple, and beet sugar, however, must be boiled with very weak sulphuric acid to convert them into glucose before the test will be applicable. There are substances in the healthy urine which interfere with the reaction in the reduction of the copper, though sugar be added in considerable quantity. Of course, this does not apply to diabetic urine. Albuminose, which, as we shall see hereafter, is produced during gastric digestion, interferes also with Trommer's test, as noted by Longet, though Dalton pointed out first the fact of the products of stomach digestion having this curious effect. With the above qualifications, Trommer's test is very reliable and easily applied. Other tests, such as those of Moore, Barreswil, Maumerie, Bottger, Fehling, the fermentation test, and that of torulæ, etc., are also used.

Lactose, milk sugar, so-called on account of it being found in milk, occurs also in the amniotic fluid of the fœtus, in the urine in the last days of pregnancy and first days of lactation. Milk sugar is produced in the economy in the mammary glands probably at the expense of glucose, as it does not occur in the blood. According to some chemists it is converted in the system into dextrose and galactose. In all probability, however, it is absorbed as such unchanged. Milk sugar, under the influence of a ferment, readily becomes lactic acid, which in time causes the souring and clotting of milk, the change taking place in the alimentary canal as well as out of it.

The remaining disaccharide, maltose ($C_{12}H_{22}O_{11}$), is produced in the economy, together with dextrin and glucose, in varying amounts, by the action of the saliva, pancreatic and intestinal juices upon starch, all of the maltose and dextrin being finally transformed, however, into glucose. Sugar is produced within the system as we have seen by the liver, mammary glands, etc. The greater part of the sugar found in the economy is introduced, however, either in the form of fruit, cane, or milk sugar, or is derived as we just mentioned from starch.

QUANTITY OF SUGAR IN 100 PARTS IN[1]

Cherries	18.12	Goats' milk	5.80
Juice of sugar cane	18.00	Cows' milk	5.20
Apricots	16.48	Indian corn-meal	3.71
Peaches	11.61	Rye flour	3.46
Pears	11.52	Barley meal	3.04
Sweat potatoes	10.20	Wheat flour	2.33
Beet roots	8.00	Oatmeal	2.19
Parsnips	4.50	Beef's liver	1.79

The exact manner in which sugar is elaborated by plants can not be said as yet to have been definitely established. Recent researches[2] render it highly probable, however, that the first stage in the production of sugar by plants consists in the production of formic aldehyde through the reduction of carbonic acid by the action of sunlight upon the chlorophyll of the leaves, the reaction being as follows,

Carbonic acid. Formic aldehyde. Oxygen.

$$H_2CO_3 = HC.HO + O_2$$

Now it is well known that formic aldehyde[3] when produced synthetically in the laboratory can be transformed by appropriate means first into paraformic aldehyde and then into formose, a form of sugar.[4] It is quite possible therefore that the formic aldehyde produced in the plant passes through similar stages, becoming ultimately perhaps starch or cellulose.

With the exception of the places mentioned sugar does not occur in the economy, being oxidized as rapidly as produced, it passes out of the system as carbon dioxide and water.

Glucose. Oxygen. Carbon dioxide. Water.

$$C_6H_{12}O_6 + 12O = 6(CO_2) + 6(H_2O)$$

Sugar, through its combustion, is therefore one great source of heat. Its uses in this respect will be considered, however, more particularly when the subject of animal heat is taken up.

The polysaccharides, or third kind of carbohydrates, includes such substances as starch, dextrin, glycogen, etc., and consist chemically of some multiple of $C_6H_{10}O_5$. In the case of starch, this multiple being taken as 3, its chemical composition is expressed by the formula $(C_6H_{10}O_5)_3$.

Although not crystallizable, starch is far from being an amorphous powder, it consisting, as found in the potato, for example (Fig. 10), of well marked, laminated granules of definite form.

[1] Dalton, op. cit., p. 54.

[2] Reinke, Berichte der deutschen chemischen Gesellschaft, 1881, Band 14, s. 2144.

[3] Formic aldehyde bears to methyl alcohol the same relation that aldehyde bears to alcohol, that is to say it is methyl alcohol dehydrogenated. It is usually obtained by the slow combustion of methyl alcohol brought about by an ignited spiral of platinum wire, the reaction being as follows,

Methyl alcohol. Oxygen. Formic aldehyde. Water.

$$CH_4O + O = CH_2O + H_2O$$

[4] Baer, Berichte der deutschen chemischen Gesellschaft, 1870, Band 3, s. 67.

The so-called corpora amylacea found in the brain, and formerly considered as being of the nature of starch, as their name implies are no longer regarded by chemists[1] as carbohydrates.

Starch exists abundantly in corn, wheat, oats, rice, potatoes, and indeed in almost all vegetable food. Tapioca, arrowroot, etc., so useful as articles of diet, under certain circumstances, are varieties of starch.

FIG. 10.

Grains of potato starch.

QUANTITY OF STARCH IN 100 PARTS IN[2]

Rice	88.65	Peas	37.30
Indian corn	67.55	Beans	33.00
Barley	66.43	Flaxseed	23.40
Oats	60.59	Potatoes	20.00
Rye	64.65	Sweet potatoes	16.05
Wheat	57.88	Chocolate	11.00

Starch may be produced from sugar, and under the influence of solar heat from plants by a process of deoxidation from carbonic acid as shown by the following formula:

Carbonic acid. Oxygen. Starch. Water.

$$6H_2CO_3 - 12O = C_6H_{10}O_5 + H_2O$$

The principle of the development of starch through the deoxidation of carbonic acid may be roughly illustrated in the following manner: A bunch of fresh mint being placed within a cylindrical tube containing dilute carbonic acid water standing over the pneumatic trough is exposed to sunlight. Soon the leaves of the mint will be seen covered with minute beads of gas, a small quantity of the latter accumulating at the top of the cylindrical tube. By withdrawing the mint and passing up a few bubbles of nitric oxide, a

[1] Hoppe Seyler, 1881, Phys. Chemie, s. 689. [2] Dalton, op. cit., p. 57.

dark brown vapor will appear at the top of the tube, proving that the contained gas was oxygen. Starch is insoluble in cold water, but by boiling the granules are liquefied, and, on cooling, remain fused together as a whitish, oxaline, homogeneous mass. In this condition, it is said to be "hydrated." The most important property of starch for the physiologist, however, is the readiness with which it is converted into one or more forms of sugar. Thus, if human saliva be added to boiled starch and the mixture be maintained at a temperature of 100° F., in a short time it will be converted into maltose, dextrose, and some little glucose.

Starch in its transformation into maltose passes through the intermediate stages of amylodextrin, erythrodextrin, achrodextrin, and isomaltose, the latter being isomeric with maltose. Maltose, being unabsorbable, is finally converted into glucose, and in this form of sugar appears, as already mentioned, in the blood. Inasmuch as starch is finally transformed into glucose, and as the latter is completely oxidized, starch, like sugar, is a source of energy, indeed a most important one, since one-half of our food, as we shall see, consists of starch. Glycogen, or animal starch ($C_6H_{10}O_5$), may be regarded functionally as so much stored glucose, to be drawn upon by the economy in time of need, glycogen being readily converted by hydration into the more combustible and diffusible glucose,

$$\underset{\text{Glycogen.}}{C_5H_{10}O_5} + \underset{\text{Water.}}{H_2O} = \underset{\text{Glucose.}}{C_6H_{10}O_6}$$

That such is the case is shown by the fact of the entire disappearance of glycogen from the body in starvation, it being transformed into glucose to make good the deficiency of the latter in the blood. The significance of glycogen from this point of view is further shown by its conversion into glucose by muscular work. One-half of the glycogen of the body is probably found in muscles, the remaining half in the liver. Indeed, as much as 40 per cent. of the dry solids of the latter organ may consist of glycogen. The glycogen of the economy is derived from the carbohydrates and the glucose of decomposed proteid, 100 parts of the latter yielding 45.08 parts of glucose.[1] Glycogen, so far as it is affected by the action of diastatic ferment, does not appear to differ from vegetable starch. Glycuronic acid, or d-glucuronic acid ($C_6H_{10}O_7$), allied chemically to starch and dextrin, occurs in the urine after the administration of camphor, turpentine, chloral, hydrate, etc., in a state of combination with the latter. It may be obtained by the reduction of saccharic acid with nascent hydrogen. Glycuronic acid, while resembling glucose in reducing alkaline copper solution and in rotating polarized light to the right, differs from it in not being fermentable with yeast. Lactic acid, or ethidene lactic acid ($C_3H_6O_3$), is a diatomic,

[1] Weintraud u. Laves, Zeitschrift für physiologische Chemie, 1894, Band 19, s. 632.

monobasic,[1] oxy-fatty acid. Lactic acid is often called "fermentation lactic acid" on account of being developed through the fermentation of the carbohydrates, the reaction consisting in the splitting of the glucose molecule,

$$\underset{\text{Glucose.}}{C_6H_{12}O_6} = 2\underset{\text{Lactic acid.}}{C_3H_6O_3}$$

A familiar example of such fermentation is the souring of milk, which depends upon the lactic fermentation of milk sugar. Recent experiments render it probable, however, that lactic acid is produced, to a certain extent, at least, from proteid as well as from carbohydrates. When absorbed lactic acid appears to be completely oxidized. Lactic acid is inactive to polarized light, it consisting of two acids, right ethidene lactic acid rotating the plane of polarization to the right, left ethidene lactic acid rotating it to the left, the two acids neutralizing each other therefore in this respect. Owing to the fact, however, of the left ethidene lactic acid being destroyed by penicillium glaucum when lactic acid, as such, is allowed to stand with that fungus, a means is afforded of obtaining the right ethidene lactic acid alone, or at least in sufficient quantity to rotate the plane of polarization to the right. It is in the latter form that lactic acid, called also sarco and para lactic acid, occurs in the blood muscle and elsewhere in the system. It is this acid to which is due the formation of KH_2PO_4, which causes the coagulation and acidity of muscle when the latter passes into the condition known as rigor mortis.

Among the diatomic dibasic acids[2] that occur in the system may be mentioned oxalic and succinic acids. Oxalic acid ($C_2H_2O_4$) is found in the urine and appears to be derived from the oxalates of the food rather than from the metabolism of the tissues of the body; at least recent observations[3] show that, upon a diet of meat alone or of meat, fat, and sugar, no oxalates are found in the urine. Oxalic acid, in the form of calcium oxalate, gives rise to one form of stone in the bladder and to the urinary sediments arising during acid and also alkaline fermentation. Succinic acid ($C_4H_6O_4$), found in the

[1] Lactic acid $\begin{cases} CH_2OH \\ CH_2 \\ COOH \end{cases}$ is said to be diatomic because it is derived from a diatomic alcohol, propylglycol $\begin{cases} CH_2OH \\ CH_2 \\ CH_2OH \end{cases}$ by the substitution of one atom of oxygen for two atoms of hydrogen, but monobasic, one atom of hydrogen only of the acid being replaceable by a monad element.

[2] Oxalic acid $\begin{cases} COOH \\ COOH \end{cases}$ is a diatomic acid because it is derived from a diatomic alcohol, glycol, $\begin{cases} CH_2OH \\ CH_2OH \end{cases}$ by the substitution of two atoms of oxygen for four atoms of hydrogen in the latter, and dibasic, two atoms of the hydrogen of the acid being replaceable by two monadic elements.

[3] Bunge, Lehrbuch Der Physiologischen und Pathologischen Chemie, 1894, s. 340.

spleen, thyroid, and thymus, appears to be derived from proteid putrefaction and alcoholic fermentation.

Inosite, though consisting of carbon, hydrogen, and oxygen, and the two latter elements existing in the proportion to form water, is neither a carbohydrate nor an oxy-fatty acid, but a member of the aromatic series, being hexa-hydroxybenzol ($C_6H_6(OH)_6$). It occurs in the body in the brain, muscle, liver, lungs, spleen, suprarenal capsules, testicles, and in the vegetable kingdom in beans and unripe peas. Nothing is known as to its origin. When introduced into the system inosite appears to be oxidized. Phenol oxybenzol[1] (C_6H_5OH), commonly called carbolic acid, though an antiseptic itself, is developed normally in the intestine as one of the products of the putrefaction of proteid, probably of tyrosin. Phenol as such, or in the form of the dioxy benzols, pyrocatechin, hydroquinone, appears in the urine, together with p-cresol, p-oxyphenyl-acetic, and p-hydrocumaric acids, benzol derivatives, in the form of alkaline ethereal sulphates. Benzoic acid is an interesting member of the aromatic group, since, when introduced into the system, it combines with glycocoll to form hippuric acid, the reaction being as follows:

$$\underset{\text{Benzoic acid.}}{C_6H_5COOH} + \underset{\text{Glycocoll.}}{NH_2CH_2COOH} = \underset{\text{Hippuric acid.}}{NH(C_6H_5CO)CH_2COOH} + \underset{\text{Water.}}{H_2O}$$

The consideration of tyrosin, indol, and skatol, will be deferred until the proximate principles of the third class are taken up, as these substances, although aromatic in nature, contain nitrogen.

Fat.—Fat is an almost universal constituent of the body; it is absent, however, in the bones, teeth, the eyelids, and scrotum, elastic and unelastic fibrous tissue. It is always present, even in extreme cases of emaciation, in the orbit, and around the kidneys.

QUANTITY OF FAT IN 100 PARTS OF TISSUE.[2]

Sweat	0.001	Liver	2.4
Saliva	0.02	Muscles	3.3
Lymph	0.05	Hair	4.2
Chyle	0.2	Milk	4.3
Mucus	0.3	Cortex of brain	8.0
Blood	0.4	Medulla	20.0
Cartilage	1.3	Nerves	22.1
Bone	1.4	Spinal cord	23 6
Crystalline lens	2.0	Adipose tissue	82.7

The amount of fat as just shown varies very considerably in the tissues; thus, while in the sweat, lymph, saliva, etc., there is a mere trace of fat, more than twenty per cent. is found in the nervous system, and over eighty in adipose tissue. The whole amount of fat, according to Burdach,[3] in the body of a man weighing 80

[1] Benzol (C_6H_6) being the so-called nucleus and OH the lateral chain.

[2] Carpenter, Physiology, 1881, p. 88.

[3] Traité de Physiologie, Tome viii., p. 80. Paris, 1857.

kilograms (176 pounds) was 4 kilograms (8.8 pounds), or 5.2 parts of fat to every 100 of body.

Fat exists in the adipose tissue, for example, in the form of vesicles which are transparent and contain the oily matters.

Fat consists of a mixture of the principle known to chemists as stearin, palmitin, and olein. The first two are solid at the temperature of the body, but are held in solution by the olein. They crystallize (Fig. 11) in needle-like forms, assuming a beautiful radi-

FIG. 11.

Stearin crystallized from a warm solution in olein. (DALTON.)

atory or arborescent appearance, where fluid, fatty, oily substances under the microscope have the appearance of round globules, bright in the center, and dark at the edges. With the exception of the phosphorized fat of nervous tissues, fat does not exist combined with the other proximate principles, as we found was the case with the inorganic principles and the sugars; there is no such molecular union of fat with any principle. There is no difficulty, therefore, in extracting it from the system in a state of purity. Pressure is often the only process needed, the oil being squeezed out of the interstices of the tissues of the organ containing it.

Fats, chemically speaking, are glycerides or ethers of glycerin, that is, glycerin in which three atoms of hydrogen are replaceable by the residues of three molecules of a fatty acid. Thus, for example, stearin ($C_3H_5(C_{18}H_{35}O_2)_3$), a form of neutral fat is glycerin, $C_3H_5\begin{cases}OH\\OH\\OH\end{cases}$, in which the three atoms of hydrogen in the three hydroxyl groups are replaced by the residues of three molecules of stearic acid ($C_{18}H_{36}O_2$), thus

$$C_3H_5\begin{cases}OC_{18}H_{35}O\\OC_{18}H_{35}O\\OC_{18}H_{35}O\end{cases} = \text{stearin.}$$

In the case of olein, $C_3H_5(C_{18}H_{33}O_2)_3$, and palmitin, $C_3H_5(C_{16}H_{31}O_2)_3$, the three atoms of hydrogen in glycerin are replaced by the residues of three molecules of oleic acid, $C_{18}H_{34}O_2$, and palmitic acid, $C_{18}H_{32}O_2$.

Such being the constitution, chemically, of neutral fats, it becomes intelligible why stearin, for example, in the presence of vapor of water heated to 572° F., takes up water, and splits into glycerin and stearic acid, as follows:

Tristearin.	Water.	Glycerin.	Stearic acid.
$C_{57}H_{110}O_6$	$+ 3H_2O =$	$C_3H_8O_3$	$+ C_{54}H_{108}O_6$

The action of alkali, soda, for example, upon stearin, is another example of this process, the stearin splitting up into glycerin and stearic acid, the latter combining with the sodium to form sodium stearate or soap, as follows:

Stearin.	Soda.	Glycerin.	Sodium stearate.
$2(C_{57}H_{110}O_6)$	$+ 6NaOH =$	$2(C_3H_8O_3)$	$+ 6NaC_{18}H_{35}O_2$

Saponification, as the splitting of a neutral fat into glycerin and fatty acid is called, whether alkali be present or absent, is brought about in the system by the action of the steapsin of the pancreatic juice upon fat. It is a most important function, since the neutral fat is emulsified by the soap so formed, that is, subdivided into minute particles, thereby rendering it absorbable. In a similar manner oleic acid, sodium oleate, and other fatty acids and soaps are formed in the system. The odor of the axilla and feet is probably due to the presence of fatty acids. It is an interesting fact that, after feeding an animal with a fatty acid, the chyle will be found to contain a considerable amount of neutral fat, showing that a synthesis the reverse of saponification takes place, that is to say, the fatty acid, fed combines with the glycerin of the body, three molecules of water being lost to form neutral fat.[1] In this connection it may be mentioned that there are other monatomic, monobasic,[2] fatty acids occurring in the body, to be referred to hereafter, such as formic, propionic, butyric, and caproic acids.

[1] Munk, Virchow Archiv, 1880, Bd. 80, s. 17.

[2] A monatomic acid is so called because it is derived from a monatomic alcohol. Acetic acid ($C_2H_4O_2$), for example, being derived from alcohol (C_2H_6O) among other ways by oxidation, as follows:

Alcohol.	Oxygen.	Acetic acid.	Water.
$C_2H_6O +$	$O_2 =$	$C_2H_4O_2 +$	H_2O

Acetic acid is a monobasic acid, one atom of hydrogen being replaceable by a monad element, as in the formation of potassium acetate, according to the following reaction:

Acetic acid.	Potassic hydrate.	Potassium acetate.	Water.
$C_2H_4O_2 +$	$KOH =$	$KC_2H_3O_2 +$	H_2O

What has just been said of acetic acid is applicable to the remaining fatty acids, they all having the constitution chemically of a hydrocarbon group united with CO_2H.

QUANTITY OF FAT IN 100 PARTS OF FOOD.[1]

Chocolate nut	49.00	Salmon	4.85
Sweet almonds	24.28	Cows' milk	3.70
Indian corn	8.80	Beans	2.50
Fowls' eggs	7.00	Wheat	2.10
Mackerel	6.76	Peas	2.10
Calf's liver	5.58	Oysters	1.51
Beef's flesh	5.19	Potatoes	0.11

The fat of the body may be derived possibly to some extent from the fat of the food. Recent experiments render it improbable, however, that such is the case. Even were it so, more fat is produced in the system than can be accounted for by the fat in the food. The experiments of Persoz, Boussingault, Thomson, Lawes, Gilbert, and others upon geese, ducks, pigs, cows, etc., with reference to this point are conclusive. In the case of a cow, for example, under the observation of Voit, it was shown that, of the 2024 grammes (72 ounces) of fat in the milk, only 1658 grammes (59 ounces) could have been derived from the fat of the feed. It is evident, therefore, that the fat obtained in such cases must have been derived from either the carbohydrate or proteid material of the food. It has been proved, however, by experiments made upon dogs,[2] for example, fed upon sugar, starch, and fat, that the fat produced could not have been derived from the proteid, but from the carbohydrate material of the food. Further, such facts as the starch of plants becoming oil, of sugar being readily transformed into alcohol and fatty acids, of carbohydrate principles constituting a part of a fattening diet, there can be no doubt that the fat produced in the economy is, under certain circumstances, largely derived from the carbohydrates present in the food. On the other hand, it is a matter of every-day observation that animals are best fattened on a feed consisting of proteid as well as of carbohydrate food stuffs, which renders it probable that fat may be derived from proteid, as well as carbohydrate principles. Indeed, as shown by Pettenkofer and Voit,[3] so far from the fat produced in the body being proportional to the carbohydrate ingested, which ought to be the case upon the supposition that fat is derived from the latter, the fat deposited is proportional to the amount of proteid destroyed. Thus, for example, in experiments made upon dogs fed with starch, although the amount of the latter given was much greater in one animal than the other, the amount of fat deposited was nevertheless in each animal about the same, showing that the fat could not have been derived from the starch, but from the proteid destroyed. This becomes intelligible if we suppose that the starch, after conversion into sugar in the economy, is oxidized and leaves the system as carbon dioxide and water, and

[1] Payen, from Dalton, op. cit., p. 62.

[2] Rubner, Zeits. für Biologie, Band 22, 1886, s. 272.

[3] Zeits. für Biologie, Band ix., s. 435, 1873. Hermann, Physiologie, Sechster Band, s. 252, 1881.

that of the proteid of the body decomposed, the non-nitrogenous part is retained within the economy as fat, the nitrogenous eliminated as urea. In further confirmation of this view it was also shown by Pettenkofer and Voit[1] that, in the case of dogs fattened upon a meat diet, the fat was derived from the proteid of the food, rather than from that of the body as in the previous experiments, but in the same manner. Apart from experimental evidence, such as that just mentioned, there are a number of general facts which confirm the view that fat may be derived from proteid as, for example, the fatty degeneration of the tissues, the conversion of dead bodies into adipocere, the development of fats out of peptones, the derivation of fatty acids and substances like acetone (CH_3COCH_3) from proteid, that in phosphorus poisoning as the fat increases the albumin diminishes, etc.

General considerations and experiments showing then that the fat deposited in the body may be derived from proteid, it may be asked of what use then are the carbohydrate principles always present in fattening diet; in what way do they contribute toward the production of fat? Regarding these principles as a source of heat to the economy, their *rôle* as a part of fattening diet becomes perfectly clear, since in being burned they save the fat otherwise derived and which would be drawn upon for the same purpose if they were absent. Hence, the fact of a dog fed on sugar and meat, excreting less urea and getting fatter than when fed on meat alone, of the negroes getting fat during the extraction of the sugar from the cane; of dogs fed on meat and rubol, palm oil, or stearin, getting fat, the sugar or oil given with the food in these instances saving the fat otherwise produced from the proteid from being burned. The carbohydrate principles evidently then play in the production of fat this secondary *rôle* of saving the fat, otherwise produced, from being consumed.

If the view of the origin of fat, just referred to, be accepted, it becomes intelligible why individuals become fat whatever they eat, and that if the fat of the body is to be reduced, all kinds of food must be diminished, as little eaten as possible, to cut off the supply, and plenty of active exercise taken to quicken the circulation and respiration, and in that way burn off that already deposited. Fat is never discharged from the body in health except in the butter of milk, but is destroyed, burnt, passing away as carbon dioxide and water; and, therefore, like sugar, being a source of heat and energy:

Fat.		Oxygen.		Carbonic acid gas.		Water.
$C_{57}H_{110}O_6$	+	O_{163}	=	$57(CO_2)$	+	$55(H_2O)$

Fat is useful also as serving to support the organs, like the eye and kidney. It fills up the spaces between vessels, bones, and muscles, rounding off the trunk and extremities into the graceful curves of the human form.

[1] Zeits. für Biologie, 1869, 1870, 1871.

It prevents the loss of heat through its bad conductive power. This function of fat is well shown in the cetacea, of which the whale, dolphin, and porpoise are examples. Such animals, being provided with an immense layer of fat just beneath skin, are enabled thereby to retain largely their heat.

Cholesterin ($C_{26}H_{44}O$), although consisting of carbon, hydrogen, and oxygen, with the hydrogen in excess and fatty to the touch, appears to have the constitution chemically of a monatomic alcohol ($C_{26}H_{43}OH$). Cholesterin is found in nervous tissue, blood corpuscles and bile, and will be referred to again in connection with the latter.

CHAPTER III.

PROXIMATE PRINCIPLES OF THE THIRD CLASS.

This class includes such substances as serum, albumin, fibrinogen, casein, hæmoglobin, mucin, keratin, urea, lecithin, pepsin, etc. They agree with the principles of the second class in being of organic origin, that is elaborated by organized bodies out of materials derived directly or indirectly from the mineral and vegetable worlds.

The water, carbon dioxide, and salts found in the mineral inorganic world, constituting the food of plants, with some exceptions, like the fungi, are converted by the plant through the agency of the sun's light and heat into such principles as starch, sugar, vegetable albumin, fibrin, and casein, etc. The plants in time serve as food for herbivorous animals, which are eaten by the carnivorous ones, while, as we shall soon see, all three, plants, herbivora, and carnivora, together with the inorganic principles, enter into the food of man.

It will be seen, therefore, that, so far as the organic principles are concerned in nature, the plant is indispensable as preparing the food for the animal; the former living on carbon dioxide, salts, etc., which would be starvation to the latter.

While the organic principles are usually developed in the order indicated, it must be mentioned, however, that chemists have succeeded in artificially preparing some of the principles of the third class, as well as those of the second, from the direct combination of the inorganic elements in the laboratory by purely physico-chemical processes, without invoking in any way the aid of a vital force in the case of either plant or animal.

The proximate principles of the third class, with some exceptions to be mentioned hereafter, differ, however, from those of the first and second classes in not being crystallizable.

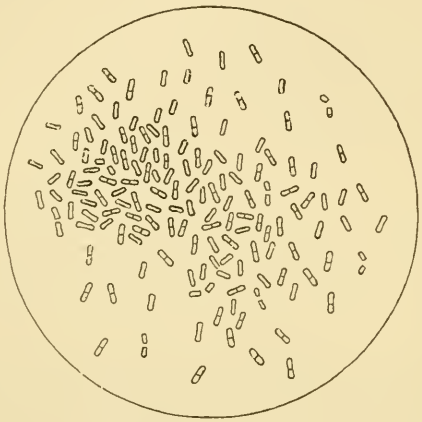
The proximate principles of the third class, however, are distinguished in a marked degree from those of the first and second in containing nitrogen. This element seems indispensable to the composition of a body exhibiting life. As is well known, those substances which are very changeable, decomposing suddenly, like nitrogen iodide, nitrogen chloride, nitroglycerin, fulminating salts, gunpowder, etc., owe their peculiar properties to the nitrogen they contain.

As we proceed in our studies, we shall see that the essence of life is in change. To make use of a homely simile, nitrogen seems to play the same part in the living body as that by a restless, excitable spirit in the living community; ever ready himself to be affected

by slight changes and to influence in the same way those around him.

Thus an important feature of the nitrogenized proximate principles is the readiness with which they undergo putrefaction—the latter being brought about by the growth and multiplication of a minute protist, the Bacterium termo (Fig. 12), just as sugar is decomposed into alcohol and carbonic dioxide through the influence of the yeast cell.

FIG. 12.



Cells of Bacterium termo; from a putrefying infusion. (DALTON.)

The effect of the bacterium cells in inducing putrefaction in this manner, like that of the saccharomyces or yeast cell in producing fermentation, is usually said to be due to catalysis. The word catalysis meaning literally to dissolve, break up, while frequently made use of in speaking of those actions in the economy which are of this character, is, however, only a word, not an explanation—in fact, merely a convenient way of expressing our ignorance of the phenomena to be explained.

The susceptibility of these organic principles to change, in and out of the body, is not only due to the nitrogen they contain, but probably to the great number of atoms entering into their composition.

It is more natural that hæmoglobin ($C_{636}H_{1025}N_{164}FeS_3O_{181}$), consisting of 2010 atoms, should break up into its constituent parts on the slightest change taking place in the surrounding conditions, than sodium chloride or water, composed of two or three atoms respectively. It is easier for two or three persons to get along together than 2010, especially when among the latter there are 164 (the nitrogenous atoms) most unstable ones.

The organic principles of this class are always combined with the inorganic ones, the union being most intimate, so much so that

as the first are used up and become effete, and are cast out of the body, the inorganic principles go with them. Like the principles of the second class, those of the third class are destroyed in the system, never appearing in the excretions in health (with the exception of casein of milk, mucus, epithelium, and epidermis). Being transformed into carbon dioxide, water, urea, etc., through a process of splitting, with subsequent oxidation, they are also a source of heat to the economy like the principles of the second class.

It is impossible to offer a classification of the nitrogenous substances occurring in the human body, since the only bond which unites all of them is the nitrogen they contain, whereas the differences depending upon chemical constitution, mode of derivation, etc., widely separate them. In endeavoring to give some account of these substances, we will consider them successively in groups, associating together such substances as agree in their chemical constitution, so far as is known, in their general properties, mode of derivation, etc. From this point of view, inadmissible, perhaps, from a purely chemical standpoint, useful, however, for purpose of description, the proximate principles of third class, those in which nitrogen is present, may be divided into the following groups: proteins, amides, amines, imides, lactic acid, and triatomic alcohol derivatives, xanthin bodies, benzol derivatives, ferments, etc.

It need hardly be added, after what has been already said, that the above groups can not be regarded as physiologically equivalent or placed in the same chemical category, as some of the substances constituting them, as we shall see hereafter, are derived from the decomposition of protein bodies, some by substitution of residues, others again in a way which is as yet unknown. We will begin our study of the proximate principles of the third class with that of the protein group.

The protein group of nitrogenous principles constitute the chief mass of the tissues, hence the name from $\pi\rho\omega\tau\epsilon\acute{\upsilon}\omega$ to be preëminent. Protein substances, generally speaking, consist of carbon, hydrogen, nitrogen, oxygen, and usually sulphur; phosphorus iron and copper, being also occasionally present. When heated, protein bodies decompose, giving rise to inflammable gases, ammoniacal compounds, carbon dioxide, water, nitrogenized bases, etc., and when thoroughly burned, first to a mass of carbon and then to an ash consisting principally of calcium and magnesium phosphates. In the present state of physiological chemistry it is impossible to classify the protein substances satisfactorily. The following classification, based more especially upon those of Hammarsten[1] and Chittenden,[2] will suffice at least for convenience of description.

[1] A Text-Book of Physiological Chemistry, by Olof Hammarsten, translated by John A. Mandel, 1893, p. 14.

[2] Chittenden, Digestive Proteolysis, Cartwright Lectures, Medical Record, Vol. 45, 1894, p. 449.

- Protein Substances
  - Albuminous Bodies or Simple Proteids
    - Albumins
      - Serum-albumin
      - Lacto-albumin
      - Myo-albumin
    - Globulins
      - Serum-globulin
      - Fibrinogen
      - Myosin
      - Myo-globulin
      - Cell-globulin
    - Albuminates
      - Acid-albumin
      - Alkali-albumin
    - Proteoses and Peptones
    - Coagulated Proteids
      - Fibrin
  - Combined Proteids
    - Chromo-proteids[1]
      - Hæmoglobin
      - Myohæmatin
    - Glyco-proteids
      - Mucins
      - Mucoids
    - Nucleo-proteids
      - yielding nuclein
        - Nuclei histon
        - Cell nuclein
      - yielding paranuclein
        - Casein
        - Vitellin
  - Albuminoids
    - Keratin
    - Elastin
    - Collagen
    - Neuro-keratin

The albuminous bodies or simple proteids, while found more especially in the muscles, glands, and blood serum, occur as well in the solids and fluids of the body generally, with the exception of the tears, perspiration, and perhaps urine, in which they are either absent or only found in traces.

QUANTITY OF PROTEIDS.[2]

Substance.	Parts per 1000.	Substance.	Parts per 1000.
Cerebro-spinal fluid	0.9	Chyle	40.9
Aqueous humor	1.4	Spinal cord	74.9
Liquor amnii	7.0	Brain	86.3
Intestinal juice	9.5	Liver	117.4
Pericardial fluid	23.6	Muscle	161.8
Lymph	24.6	Blood	195.6
Pancreatic juice	33.3	Middle coat of arteries	273.3
Synovia	39.1	Crystalline lens	383.0
Milk	39.4		

Albuminous bodies consist of carbon, hydrogen, nitrogen, oxygen, sulphur, and occasionally of phosphorus, iron being generally a constituent of their ash. Their percentage composition varies, as follows:

Carbon	50.6 –54.5 per cent.
Hydrogen	6.5 – 7.3 " "
Nitrogen	15.0 –17.6 " "
Oxygen	21.50–23.50 " "
Sulphur	0.8 – 2.2 " "
Phosphorus	0.42– 0.85 " "

The molecular weight of albumin not having been as yet determined, its formula can not be given. That of alkali albuminate is

[1] In order to prevent misunderstanding it may be stated that the term "proteid" as suggested by Hoppe Seyler and used by Hammarsten embraces the substances included above as chromo- and glyco-proteids.

[2] Group Besanez, Lehrbuch der Physiologischen Chemie, 1878, s. 128.

usually accepted as being approximately $C_{72}H_{112}N_{18}SO_{22}$ (Lieberkuhn).

Although the constitution chemically of albuminous bodies has not yet been established, judging from the products of decomposition, the albumin molecule consists, among other subtances, of such as have a fatty and an aromatic nature. The albuminous bodies are odorless, tasteless, and usually amorphous. Most of them are colloids, that is, do not diffuse, or if so, but slightly through animal membranes, and have a high osmotic equivalent. They rotate polarized light to the left. The presence of albuminous bodies is determined by precipitation and color tests. Thus, for example, on heating a solution of albumin to the proper temperature, the latter depending upon the nature of the albumin present, the albumin will usually separate in a solid form as crude "coagulated" albumin. It should be mentioned in this connection that the reaction of the solution containing the albumin must be acid, an alkaline albumin solution not coagulating upon heating, and a neutral one but partly and incompletely. Albuminous bodies are precipitated by the three ordinary mineral acids. Thus, for example, if an albumin solution be allowed to flow gently on nitric acid in a reagent glass, as in the performance of Heller's test, a white opaque ring consisting of precipitated albumin appears where the two liquids meet. Albuminous bodies are also precipitated by metallic salts, ferrocyanide of potassium in acetic acid solution, alcohol, tannic acid, etc.

Albuminous bodies, when heated to the boiling point, give, on the addition of nitric acid, a yellow color known as the xanthoprotein reaction. A solution of mercuric nitrate in nitric nitrous acid known as Millon's reagent, precipitates albumin in solution, giving to it a red color. Tyrosin and other benzol derivatives give the same reaction with Millon's reagent, confirming the view that the albumin molecule contains an aromatic group. If caustic soda or potash be added to an albumin solution, and then drop by drop dilute cupric sulphate, the solution becomes just reddish, then reddish violet, and lastly violet blue, the reaction being known as the Biuret test. In testing for albumin, as no one test is characteristic, it is hardly necessary to add that several precipitate and color tests should be made use of.

Albumins.—These substances are soluble in water, coagulate by boiling and on standing with alcohol. They are very rich in sulphur, containing 1.6 to 2.2 per cent. Serum-albumin, lacto-albumin, and myo-albumin are found respectively as proteid constituents of blood, plasma, milk, and muscle. Serum-albumin usually taken as the type of the albumins, as obtained from the blood of the horse, consists chemically of C53.06, H6.85, N16.04, S1.80, O22.26.[1] It is found in the lymph exudations generally as well as in the blood.

If a solution of serum-albumin having a neutral or acid reaction

[1] Hammarsten, op. cit., p. 62.

be heated to 70°–75° C. it will coagulate, that is will be precipitated in an insoluble form. As it appears, however, that heating at temperatures of 73°, 77° and 84° C. gives three distinct coagulations, it is possible that the substance now known as serum-albumin may really consist of three distinct proteids. An important property of serum-albumin is that it is not precipitated by the addition of magnesium sulphate ($MgSO_4$) to a liquid containing it. Advantage is taken of this to separate serum-albumin from serum-globulin, both of which exist together in the blood-globulins. These albuminous bodies are insoluble in water, but soluble in dilute neutral salt solutions. They coagulate by heating. Serum-globulin and fibrinogen are found in blood plasma and lymph. Myosin, the principal proteid constituent of dead muscle, exists in living muscle apparently in the form of a promyosin or myosinogen. Myoglobulin, also found in muscle, bears to the latter very much the same relation that serum-globulin bears to blood plasma. Cell-globulin is found in cells.

Serum-globulin, often called para-globulin, as derived from horse's blood, consists chemically of C52.71,H.7.01,N15.85,S1.11,O23.24.[1] It is found in the blood, as already mentioned in lymph, and the exudations generally. Serum-globulin in solution is precipitated not only by magnesium sulphate, but also by sodium chloride (NaCl), incompletely, however, by the latter. In neutral or feebly acid solutions, serum-globulin coagulates at a temperature of 75° C. Fibrinogen, one of the most important of the globulins as derived from horse's blood, consists chemically of C52.93,H.6.90,N16.66,-S.1.25,O.22.26.[2] It is found in the liquor sanguinis lymph and at times also in the exudations.

Fibrinogen differs from serum-globulin in coagulating at a lower temperature, 56° to 60° C., and on being as completely precipitated by sodium chloride as by magnesium sulphate. As we shall see hereafter, it is regarded as giving rise to the insoluble proteid fibrin at the moment of the coagulation of the blood.

Albuminates.—Acid albuminate, acid albumin, or syntonin, as it is sometimes called, is produced by the action of diluted hydrochloric acid upon proteid as takes place in the stomach, in the digestion of albuminous food by the gastric juice, the latter containing hydrochloric acid. Alkali albuminate is formed by the action of alkali upon albuminous bodies as in the instance of the alkali of the intestine acting upon proteids. Acid and alkali albuminates are nearly insoluble in water, but are soluble in dilute acid and alkali.

Proteoses and Peptones.—Proteoses and albumoses, as they are also called, may be regarded as propeptones occurring during the digestion, of albuminous food as intermediary products between albumin and peptone in so far as they are not albuminates. Peptones are the final products of the decomposition of albuminous

[1] Hammarsten, op. cit., loc. cit.
[2] Hammarsten, op. cit., loc. cit.

bodies, brought about by means of ferments, or possibly in other ways. Proteoses are usually separated from peptones by saturating the solution containing them both with ammonium sulphate, the proteoses being precipitated, the peptones remaining in solution. It should be stated, however, that, according to Neumeister, the deuteroproteose occurring in pepsin digestion is not precipitated by ammonium sulphate.[1]

Coagulated Proteids.—These bodies, of which fibrin is an example, are insoluble in water, alcohol, dilute acids and alkalies, salt solutions, but soluble in pepsin, hydrochloric acid, strong acids and alkalies, and alkaline solutions of trypsin.

Combined Proteids.—This group of protein substances is more complex than the albuminous bodies or simple proteids just considered. They consist, as their name implies, of proteid combined with non-proteid bodies, such as coloring matters, carbohydrates, nucleic acid.

Chromo-proteids.—These substances consist of proteids combined with a pigment containing iron, such as hæmoglobin, the coloring matter of the red blood corpuscles and its derivatives, to be referred to again, and histio-hæmatin or myo-hæmatin, found especially in the muscle and regarded as existing in two forms, myohæmatin and oxy-myohæmatin, corresponding to the hæmoglobin and oxy-hæmoglobin of the blood.

Glyco-proteids.—These are proteids combined with carbohydrates as in mucins, substances found in mucous glands, goblet cells, cement substance, epithelium, connective tissue. Mucins are colloidal substances, mucilaginous and thready when in solution. They are insoluble in water, soluble in very weak alkalies, precipitated by acetic acid and yield, when treated with a mineral acid, a substance capable of reducing a copper oxy-hydrate. The latter property is an important one, since, by means of it, mucins are distinguished from substances closely resembling them in their properties. Mucin, as derived from the sub-maxillaries, consists, according to Hammarsten,[2] of C.48.84, H.6.80, N12.32, S0.84, O.31.20. It may be mentioned that while mucin agrees in composition with the simple proteids in consisting of the same chemical elements it contains less nitrogen and usually less carbon. Mucin substances are usually divided into mucins and mucoids. This classification is, however, an arbitrary one, as there are intermediate substances which make it difficult to define two such groups. Among the so-called mucoids may be mentioned chondro-mucoid found in muscle, the colloid matter of certain tumors, the pseudo-colloid of ovarian cysts; the two latter being, however, pathological in nature.

Nucleo-proteids.—These substances are found in the cells of both the vegetable and animal kingdoms. They are characterized more especially by yielding through the action of pepsin, hydrochloric

[1] Hammarsten, op. cit., p. 28.
[2] Op. cit., p. 32.

acid, phosphorized substances, which, according as they do or do not yield xanthin, are called nucleins or paranucleins. Nuclein occurs as nucleo-histon in the leucocytes of the blood and as the chief constituent of cell nuclei, paranuclein in casein, vitellin, etc. The supposed importance attached to nucleo-histon as a factor in the production of the coagulation of the blood will be considered hereafter.

Albuminoids.—The substances embraced together as the third class of protein bodies differ so among themselves that they cannot be regarded as a natural group. The albuminoids agree, however, in constituting important parts of the skeleton and being found generally in the economy in an insoluble state and in resisting the action of reagents, particularly of those which dissolve albumins. The albuminoids are derived in the economy from the proteids, but do not appear to be convertible into the latter.

Keratin.—This substance is the chief constituent of epidermis, hair, and nails, and in the modified form of neuro-keratin is found in the brain and the medullary sheath of nerves. As found in the hair keratin consists of carbon, hydrogen, nitrogen, oxygen, and sulphur, being very rich in the latter. Part of the sulphur, at least, appears to be in a loose state of combination, lead combs becoming black by long usage through formation of lead sulphide.

Elastin.—This albuminoid is found in the connective tissues and in some cases, as in the ligamentum nuchæ, to such an extent as to constitute a special tissue. The elastic tissue in the ligamentum nuchæ of the giraffe and elephant is much developed. The ligamentum nuchæ in the giraffe dissected by the author measured *in situ* more than 9 feet, 6 feet of which, after removal from the body, contracted to 4 feet. Elastin differs chemically from keratin in containing very little, if any, sulphur. Elastin is very insoluble in boiling water and in most reagents.

Collagen.—This substance is the principal constituent of the connective tissues and as ossein of the organic substance of bone. It is found also in cartilage, more or less mixed with the substances constituting its chemical basis, the so-called chondrigen. Collagen can be obtained from bones by treating the latter with hydrochloric acid, which dissolves the earthy matters, and then removing the acid with water. Collagen consists chemically, according to Hofmeister,[1] of C 50.75, H 6.47, N 17.86, S + O 24.92. It is insoluble in water, salt solutions, dilute acids, and alkalies, and is converted by continuous boiling into gelatine. It will be remembered that, in addition to the protein bodies just considered, a number of other nitrogenous principles are found in the human economy that cannot be placed in the above category. To the consideration of these let us now turn, premising, however, that, as most of them will be considered again more or less in detail, a passing notice will suffice in this connection.

[1] Hammarsten, op. cit., p. 37.

Amides.[1]—Glycocoll, or amido-acetic acid (CH_2NH_2COOH), occurs in bile combined with cholic acid as sodium glycocholate, and in the urine combined with hippuric acid as benzoic acid, and with phenyl acetic acid as phenaceturic acid ($C_{10}H_{11}NO_3$). The amides, leucin, lysin, tyrosin, aspartic acid, are normal products of the digestion of proteids by the trypsin of the pancreatic juice. Leucin, chemically speaking, is amido-caproic acid[2] ($C_5H_{10}(NH_2)COOH$); lysin, diamido-caproic acid ($C_6H_{11}(NH_2)_2COOH$); tyrosin, p-oxy-phenyl-amido-propionic acid ($HOC_6H_4C_2H_3(NH_2)COOH$); aspartic acid, amido-succinic acid ($C_2H_3(NH_2)COOH$). Taurin, or amido-ethyl-sulphonic acid ($NH_2C_2H_4SO_2OH$), occurs in the bile in combination with cholic acid as sodium taurocholate. Urea (CON_2H_4), or carbamide, regarded as a diamide, consists of the residue of one molecule of carbon dioxide and two molecules of ammonia in which two atoms of hydrogen are replaced by one of oxygen.

Ammonia. Urea.

$$N_2\begin{cases}H_2\\H_2\\H_2\end{cases}\quad CO\begin{cases}NH_2\\NH_2\end{cases}$$

Amines.[3]—Among the amines occurring in the body may be mentioned the amines of the olefines,[4] cholin and neurin, derivatives of lecithin. Cholin chemically is trimethyl oxy-ethyl ammonium hydroxide $(CH_3)_3\equiv N\begin{cases}OH\\CH_2CH_2OH\end{cases}$. Neurin, differing in its chemical composition from cholin in containing one molecule less of water, is trimethyl-vinyl ammonium hydroxide, $(CH_3)_3\equiv N\begin{cases}OH\\CH=CH_2\end{cases}$ and is a powerful poison. As a matter of general interest it may be mentioned in this connection that ptomaines, basic substances produced from proteid by bacterial putrefaction, are olefine amines, the poisonous ones being called toxines. Thus, for example, putrescin occurring in the urine and feces in cystitis is chemically tetra-methylene-diamin ($H_2N(CH_2)_4NH_2$). Cadaverin, found in cholera feces, is penta-methylene-diamin

[1] An amide may be regarded as ammonia, in which an atom of hydrogen is replaced by a residue. Thus, for example, acetamide (C_2H_5ON) is ammonia in which an atom of hydrogen is replaced by the residue of acetic acid as follows:

Ammonia. Acetamide.

$$N\begin{cases}H\\H\\H\end{cases}\qquad N\begin{cases}C_2H_3O\\H\\H\end{cases}$$

[2] Leucin is regarded by some chemists as being rather iso-butyl-amido-acetic acid.

[3] An amine or compound ammonia may be regarded as ammonia in which one or more atoms of hydrogen are replaced by one or more alcoholic radicals, such as methyl, ethyl, etc. Thus

Ammonia. Ethylamine. Triethylamine.

$$N\begin{cases}H\\H\\H\end{cases}\qquad N\begin{cases}C_2H_5\\H\\H\end{cases}\qquad N\begin{cases}C_2H_5\\C_2H_5\\C_2H_5\end{cases}$$

[4] Olefines include such hydrocarbons as ethylene (C_2H_4), propylene (C_2H_6).

($H_2N(CH_2)_5NH_2$). Leucomaines, as distinguished from ptomaines, are the products of protein substance brought about, however, not by micro-organisms, but by the metabolism or the normal exchange of material constantly going on in the economy. Some leucomaines being poisonous in small doses, their accumulation in the system, through imperfect excretion or oxidation, is regarded by many clinicians as a source of disease, of auto-intoxication.

Imides.—Of the imide derivatives of the body may be mentioned, creatin and creatinin, and their homologues, lysatin and lysatinin, derivatives of guanidin, the imide of urea,[1] $HN = G\begin{cases} NH_2 \\ NH_2 \end{cases}$. Thus creatin found in the muscles, blood, and urine is methyl guanidin acetic acid, $HNC\begin{cases} NH_2 \\ N(CH_3)CH_2COOH \end{cases}$. Creatinin, readily derived from creatin, differing from it only in containing one less molecule of water, is glycoyl methyl guanidin, $HNC\begin{cases} NH—CO \\ N(CH_3)CH_2 \end{cases}$. Lysatin ($C_6H_{12}N_2O_2$) and lysatinin ($C_6H_{11}N_3O_2$), regarded as homologues of creatin and creatinin, are products, like the latter, of the decomposition of the proteid of either the food or the body.

Lactic Acid Derivatives.—Cystin ($C_6H_{10}N_2O_4S_2$) is an interesting member of this group, giving rise occasionally to the formation of stone in the bladder. It is derived by oxidation of cysteïn, the latter being a derivative of lactic acid through the substitution of NH_2 and SH for H and OH in the former. Thus

Lactic acid.	Cysteïn.
H	NH_2
|	|
$CH_3—C—COOH$	$CH_3—C—COOH$
|	|
OH	SH

Triatomic Alcohol Derivatives.—Lecithin is regarded as being a member of this group, as it is resolved either naturally or artificially into cholin, fatty acid, and glycero-phosphoric acids, the latter being glycerin or triatomic alcohol, in which one hydroxyl group is replaced by the residue of phosphoric acid. Thus

Glycerin.	Glycero-phosphoric acid.
$C_3H_5\begin{cases} OH \\ OH \\ OH \end{cases}$	$C_3H_5\begin{cases} PO_4H_2 \\ OH \\ OH \end{cases}$

As the fatty acid entering into the constitution of the lecithin molecule is not always the same, there will be different kinds of lecithin, according to the kind of fatty acid that the lecithin contains—oleic, palmetic, stearic. Thus, for example, in the particular kind of lecithin, known as distearyllecithin, consisting, according to Hammarsten,[2] of

$$C_{44}H_{90}NPO_9 = HO(GH_3)_3NG_2H_4O(OH)POOG_3H_5(C_{18}H_{35}O_2)_2$$

[1] Imides are compounds of NH. [2] Op. cit., p. 43.

The fatty acid element present, as the name implies, is stearic acid $(C_{18}H_{35}O_2)_2$, the cholin and glycero-phosphoric constituents being represented by $HO(CH_3)_3NC_2H_4O$, and $O(OH)POOC_3H_5$, respectively. Lecithin is found universally throughout the body, being present in all cells, the muscles, blood, lymph, bile, milk, and especially in the tissues of the nervous system. The oily drops and threads, the so-called myelin forms of the latter, observed under the microscope, are due to the swelling up of lecithin in water. Lecithin has a waxy appearance and is soluble in alcohol and ether. Through putrefaction it breaks up in the intestine into its constituents, which, under certain circumstances, appear to be absorbed. Lecithin in combination with cerebrin forms protagon. The chemical constitution of cerebrin has not yet been established; it is a nitrogenous substance, apparently free from phosphorus and is, as already mentioned, a glucoside, yielding that form of sugar already described as galactose.

Protagon.—A nitrogenized phosphorized substance with the empirical formula according to Gamgee[1] of $C_{160}H_{308}N_5PO_{35}$ is the chief constituent of the white substance of the nervous system, being found especially in the brain.

Xanthin Bodies.—This group includes xanthin, guanin, hypoxanthin, adenin, etc.; substances which by their chemical constitution are closely related to each other and to uric acid. Thus xanthin $(C_5H_4N_4O_2)$ differs from uric acid $(C_5H_4N_4O_3)$ in containing one atom less of oxygen. It gives rise occasionally to a form of stone in the bladder of exceeding hardness. Guanin $(C_5H_5N_5O)$ is imido-xanthin, that is xanthin with one atom more of hydrogen and nitrogen but one atom less of oxygen. Hypoxanthin, or sarcin $(C_5H_4N_4O)$, is uric acid with two atoms less of oxygen.

Adenin (C_5H_5N), or imido-sarcin, differs from sarcin in containing one atom more of hydrogen and nitrogen and also in being oxygen free. The xanthin bodies are found in small quantities in the urine, and in the fluids and tissues of the body generally, nuclein, it being remembered, yielding xanthin.

Benzol Derivatives.—Indol and skatol, members of this group, are found normally in the alimentary canal as products of the putrefaction of albuminous bodies; oxidized into indoxyl and skatoxyl, respectively, they pass to the liver and thence into the urine, partly as the corresponding ethereal sulphuric and partly as glycuronic acids. Indol is chemically benzo-pyrol (C_8H_7N), and skatol, methyl-indol $(C_8H_5CH_3NH)$, that is, indol in which an atom of hydrogen is replaced by the radical methyl CH_3.

Ferments.—The ferments, or rather the unorganized ferments or enzymes, so far as their composition is understood, are nitrogenous substances, resembling in some respects albuminous bodies. These bodies are elaborated within the cells of the glands producing them, and have the power, even in very small quantities, of decomposing

[1] A Text-Book of the Physiological Chemistry of the Animal Body, 1880, p. 428.

or splitting other substances without entering into combination with them or their products. Among such enzymes may be mentioned the ptyalin of the saliva, the pepsin of the gastric juice, the steapsin of the pancreatic juice, etc., the uses of which in the digestion of food will be considered hereafter. Organized ferments, as distinguished from the unorganized or enzymes, are organized living beings, the putrefactive and fermentative processes that they give rise to being phases in the life of such micro-organisms. An enzyme, or unorganized ferment, differs, therefore, from an organized one in that its characteristic effect, such as the conversion of starch into maltose by ptyalin, is effected after separation from the cells that produced it, whereas the fermentation of glucose by the yeast fungus Saccharomyces cerevisiæ, resulting in the formation of carbon dioxide and water, is a stage in the life history of that micro-organism.

CHAPTER IV.

FOOD.

Vital like all other kind of work involves consumption of material, expenditure of energy. Portions of our tissues and the food appropriated by them are slowly but constantly consumed, with the liberation of heat or energy. The carbon dioxide and water exhaled with the breath, the urea excreted in the urine are evidences of so much food and tissue having been destroyed. Our thoughts, our words, our gestures are manifestations of the transformation of the heat or energy so set free. This daily, hourly, momentary destruction of food and tissue with the accompanying liberation and transformation of energy demands the constant renewal of the materials of which the food and tissues consist. Hence the necessity of food, by which we mean any substance, inorganic or organic, solid or liquid, that will nourish the body, renew the materials consumed in producing those forms of energy called vital.

Under ordinary circumstances the sensations of hunger and thirst are the first indications that solid and liquid food are required by the system. These sensations seem to be due to a certain condition of the stomach and mouth induced by the want of food experienced by the general system. That such is the case seems to be justified by facts like the following. It is well known that the sensations of hunger and thirst can be relieved by introducing food into the system through fistular openings made in the body by disease or wounds. Thus food taken into the system through an opening in the intestine, as is well known, will not only relieve the sensation of hunger but sustain life, and in the case of an opening into the œsophagus, when water and spirit were injected into the stomach, the thirst was relieved. It is also well known that bathing and wringing the clothes in salt water have been the means of temporarily relieving the thirst of shipwrecked sailors.

On the other hand, if the food is not absorbed, the sensations of hunger in the stomach and of thirst in the mouth are only temporarily relieved, even though solid food may be eaten and water be drank in large quantities; the general wants of the system in such cases not being satisfied.

The articles commonly made use of as food, by man, such as meat, fish, bread, potatoes, butter, eggs, milk, etc., owe their nutritive value to the five so-called food stuffs or food principles that they contain, viz., water, proteids, fats, carbohydrates, salts.[1]

[1] Albuminoids, which, we have seen, resemble in many respects proteids, are often regarded as constituting a sixth food stuff, gelatin for example being often used in the making of soup, etc. Gelatin can not, however, be said to constitute a food

COMPOSITION OF FOODS.[1]

Articles.	Water.	Proteids.	Fats.	Carbohydrates.	Salts.
Beefsteak	74.4	20.5	3.5	. . .	1.6
Fat pork	39.0	9.8	48.9	. . .	2.3
Smoked ham	27.8	24.0	36.5	. . .	10.1
White fish	78.0	18.1	2.9	. . .	1.0
Poultry	74.0	21.0	3.8	. . .	1.2
White wheaten bread	40.0	8.0	1.5	49.2	1.3
Wheat flour	15.0	11.0	2.0	70.3	1.7
Biscuit	8.0	15.6	1.3	73.4	1.7
Rice	10.0	5.0	0.8	83.2	0.5
Oatmeal	15.0	12.6	5.6	63.0	3.0
Maize	13.5	10.0	6.7	64.5	1.4
Macaroni	13.1	9.0	0.3	76.8	0.8
Arrow root	15.4	0.8	. . .	83.3	0.27
Peas (dry)	15.0	22.0	2.0	53.0	2.4
Potatoes	74.0	2.0	0.16	21.0	1.0
Carrots	85.0	1.6	0.25	8.4	1.0
Cabbage	91.0	1.8	5.0	5.8	0.7
Butter	6.0	0.3	91.0	. . .	2.7
Egg (10 per cent. deducted for shell)	73.5	13.5	11.6	. . .	1.0
Cheese	36.8	33.5	24.3	. . .	5.4
Milk (S. G. 1032)	86.8	4.0	3.7	4.8	0.7
Cream	66.0	2.7	26.7	2.8	1.8
Skimmed milk	88.0	4.0	1.8	5.4	0.8
Sugar	3.0	. . .	. . .	96.5	0.5

That the food stuffs should consist of the principles just mentioned becomes evident when it is remembered that the body which the food nourishes is made up essentially of the very same principles.

It has just been mentioned that the use of food is to repair the waste of the tissues, and through combustion in the economy to liberate energy. As the body consists of proteids, carbohydrates, fats, salts, and water, all the food stuffs must be regarded, in a broad sense, as tissue makers. The proteid or nitrogenous food stuffs supply the material for the production of proteid or nitrogenous tissue; carbohydrates, in part, are converted into fat, salts replace salts, etc. No tissue consists of any one principle, such as proteid alone, but like protoplasm of proteid in combination with salts, water, etc., hence food must consist of all the food stuffs. The importance of water and salts in this respect is often lost sight of, especially in the case of the latter, salts being usually introduced into the economy, not as such, but as constituents of the food. Deprive, however, man or animal of water and salts, and they will as surely succumb as if deprived of proteid or other food stuff. Further, while proteid food without doubt furnishes the materials for the building up of proteid tissue only a part of it, the so-called tissue

stuff in the same sense as proteid. It does not build up tissue, nor does it exist as such in any food, being prepared by boiling the collagen of bones and connective tissues. Gelatin and other albuminoids when used as food being, however, oxidized like carbohydrates and fats are in this respect of considerable value.

[1] Parkes, A Manual of Practical Hygiene, 7th edition, 1887, p. 243.

proteid, "organ eiweiss,"[1] is so applied, the remaining portion, the circulating proteid, "circulirendes eiweiss," the "luxus"[2] in the sense of proteid being only plastic, in being oxidized liberates a considerable amount of energy. On the other hand, while carbohydrates in being completely oxidized in the body like fats, must be regarded as the principal sources of energy, yet inasmuch as they are converted into fat they must be regarded in this sense at least as tissue makers. No sharp line of demarcation can then be drawn between the different kind of food stuffs. They certainly can not be divided as they were formerly by Liebig[3] into two classes, plastic and calorifacient. All that can be stated is that while the food stuffs make tissue, the water and salts, however indispensable from the latter point of view, do not liberate energy, leaving the body in the same condition as introduced.

It is well known that while carbohydrates and fats are completely oxidized in the economy, more heat is produced by the burning of fat than of an equal weight of starch, 1 part of fat being equal in this respect to 2.2 or 2.4 parts of starch. That is to say fat may replace in the diet more than twice its weight of carbohydrate, the ratio being called the isodynamic equivalent. Taking into consideration that proteid food is imperfectly burned in the body and deducting the heat that would be liberated by burning the urea 1 part of proteid would replace in the diet 1.2 to 1.3 parts of starch. When compared from this point of view the nitrogenous matter constitutes 22 per cent., the non-nitrogenous ones 78 per cent. of the food, being therefore in the proportion of 1 to 3.55. From such considerations and as confirmed by experience it has been shown that, apart from 1530 grammes (54 oz.) of water drunk as such, life can be best maintained in a state of health on a diet consisting of: water, 559 grammes (19 oz.) derived from the food; proteids, 130 grammes (4.6 oz.); fats, 100 grammes (3.5 oz.); carbohydrates, 300 grammes (10.5 oz.); salts, 20 grammes (0.7 oz.). The proportion in which the proteids, fats, and carbohydrates may replace each other in a daily diet upon the principles just explained is shown according to different authorities in the following table:

DIET OF FOOD STUFFS.

	Moleschott.	Ranke.	Voit.	Atwater.
Proteid . .	130 grammes	100 grammes	118 grammes	125 grammes
Fats . .	40 "	100 "	56 "	125 "
Carbohydrates	550 "	240 "	500 "	400 "

It will be observed that according to Voit the nitrogenous are to the non-nitrogenous food stuffs in the proportion of 1 to 4.7, in the

[1] Voit in Hermann, Handbuch der Physiologie, Band vi., s. 300, 1881.

[2] Lehmann (Wagner: Handwörterbuch, 1884, ii., s. 18). Frerichs (Archiv f. Anat. und Phys., 1848, s. 469). Bidder u. Schmidt (Die Verdauungssäfte, 1852, s. 348).

[3] Die Organische Chemie, 1842. Ann. d. Chemie u. Phar., xli., 1842; liii., 1845; lviii., 1846; lxx., 1849; lxxix., 1851.

daily diet. As our daily food does not actually consist, however, of proteid, carbohydrates, etc., but of bread, meat, and such articles, it becomes as important to determine the quantity and quality of the food with which the economy should be supplied in order to maintain a state of health as that of the food stuffs. Indeed, as a matter of fact, the proper proportion in which food stuffs should be present in a normal diet is determined from the nature of the ingesta, that is the food eaten, and the egesta. As the various kinds of food contain more or less the different food stuffs it might naturally be supposed that it was immaterial whether man lived upon animal or vegetable food. As a matter of fact, as we shall see hereafter, proteid food is converted by digestive processes into peptone, whether derived from beef or potatoes, fats and salts are assimilated by the economy, whether supplied by the eating of fish or rice. As vegetable foods are characterized by being rich in carbohydrates and relatively poor in proteids and fats, animal foods in being rich in proteids and fats, and relatively poor in carbohydrates, it follows that the economy upon a diet restricted to either one or the other kind of food will receive either too much carbon or too much nitrogen. This will become evident from a consideration of the amount of the carbon and nitrogen supplied to the economy upon an exclusively bread or meat diet in a state of health.

RATIO OF CARBON TO NITROGEN IN EXCRETA.

	Carbon.	Nitrogen.
Respiration . .	248.8 grammes.	0 grammes.
Perspiration . .	2.6 "	0 "
Urine . . .	9.8 "	15.8 "
Fæces . . .	20.0 "	3.0 "
	281.2	18.8

There are found in the excreta 281.8 grammes of carbon and 18.8 grammes of nitrogen, the carbon being to the nitrogen in the proportion of nearly 15 to 1.

$$\frac{C = 281.2}{N = 18.8} = 14.9.$$

Such being the case, it will be seen that, upon a diet restricted to bread, in order that the economy should receive 19 grammes of nitrogen, 1944 grammes of bread would have not only to be eaten but assimilated, the system then receiving 30 grammes of carbon to 1 of nitrogen, or twice as much carbon as necessary.

281.2 grammes of carbon and 18.8 grammes of nitrogen are found in the excreta, or 15 C to 1 N.

1944 gr. of bread contain 583 gr. C and 19.4 gr. N, or 30 C to 1 N.
2981 gr. of meat contain 298 gr. C and 89.7 gr. N, or 3 C to 1 N.
990 gr. (2 lbs.) of bread contain . C 300 gr. and N 9.9 gr.
337 gr. (¾ lb.) of meat contain . . C 30 gr. and N 9.9 gr.

1327 gr. of bread and meat contain . C 330 gr. and N 19.8 gr.
or C 16.6 to N 1.

On the other hand, if the food consists of meat alone, then in order to obtain the necessary 281 grammes of carbon as much as 2981 grammes of meat would have to be eaten, the economy receiving then three grammes of carbon to one of nitrogen, the amount of carbon being then one-fifth of what it ought to be, relatively to the nitrogen, and the latter in amount absolutely five times too great. If, however, bread and meat be eaten in the proportions given in the table, then the economy will receive for about sixteen grammes of carbon one gramme of nitrogen, the ratio differing a little from that of the excreta, as might be expected, the food of the man consisting, as we shall see, of other articles as well as of bread and meat. In the latter case when the carbon and nitrogen of the ingesta and egesta balance each other, and, indeed, the salts and water as well, the economy is then said to be in a state of carbon and nitrogen equilibrium. It should be mentioned, in connection with the example just given of a diet restricted to meat, that, as a matter of fact, life cannot be maintained upon such a diet. As more than 2.2 kilogrammes (4.8 lbs.) of meat must be eaten and digested by a man in 24 hours in order to obtain the 280 grammes of carbon, a task is imposed upon the digestive organs that they cannot perform. A man soon succumbs upon a purely meat diet, drawing upon the fat of his own body to supply that which should be present in his food. Even a carnivorous animal, like a dog, whose alimentary apparatus is especially adapted to digest meat, can only be kept alive upon a purely meat diet, when fat and muscular at the beginning of the experiment, and when the meat eaten is equal to the $\frac{1}{20}$ or $\frac{1}{25}$ of the weight of the body, a diet which increases enormously the excretion of urea, a condition far from physiological. On the other hand, if the food consists of fat alone, man or beast will live but a short time, and it is worthy of mention that on such a diet less urea is excreted than in the starving condition, the albuminous tissues, the source of the urea, being spared through the oxidation of the fat. If more fat, however, be taken than can be disposed of in this way, as shown by the retention of carbon in the system, then fat is stored up and the albuminous tissues destroyed. The effect of a carbohydrate diet is essentially the same as a fatty one, sugar or transformed starch being, however, more readily oxidized than fat, seventeen parts of sugar being equal to ten parts of fat in this respect; less urea is, therefore, excreted upon a carbohydrate diet than upon a fatty one. A certain amount of body fat appears to be also destroyed upon a carbohydrate diet.

Of all foods, milk is the one which combines in itself to the greatest extent the proper substances in quantity and quality for the nutrition of the body, and were life limited to its early periods, it might be stated that milk alone would suffice for the maintenance of life; as the child, however, develops into the adult necessity is felt for other kinds of food as well. All through life, however, milk constitutes a most important article of diet, and can be more relied upon, both in sickness and in health, than any other kind of food.

While life can not be maintained upon any one article of diet, under certain circumstances the latter may with advantage be restricted largely, though not exclusively to some one kind of food. Thus, for example, certain wild tribes in South America subsist almost entirely upon beef. The latter supplies sufficient material for the repair of the tissues, and liberates enough heat to replace the little lost by the body, the climate being warm, and to supply the energy expended in their daily life. In the arctic regions, however, where the temperature may fall as low as —72° F. and the body loses heat very rapidly, the food consists principally of oleaginous substances, blubber, fat, etc. These substances in producing, through combustion in the economy, a great quantity of heat are therefore especially suited as articles of diet. On the other hand, in certain parts of the tropics, where the temperature may be as high as 140° F., the body losing but little heat, the staple food, as might be expected from what has just been said, is rice or dates, which produce relatively little heat.

In addition to what has already been said in reference to the excreta and nutritive value of particular kinds of food, it might also be inferred, from the fact of the teeth of man being of both the carnivorous and herbivorous types and of his alimentary canal being intermediate in character between that of the carnivora and herbivora, that the food should be of a mixed kind. The quantity of food that a man can eat and live is very different, as might be supposed, from that which he should eat. On the one hand, a young Esquimaux is said to have eaten as much as thirty-five pounds of food in twenty-four hours; on the other that the daily food of Thomas Wood consisted for eighteen years of sixteen ounces of flour made into a pudding with water. Leaving out of consideration such extreme cases, experience has shown that a man in full health and taking active exercise in the open air may subsist for a considerable time upon a diet consisting of: meat, 453 grammes (16 ounces); bread, 540 grammes (19 ounces); butter or fat, 100 grammes (3.5 ounces); water, 1530 grammes (51 ounces). In order, however, that health should be maintained continuously, the above diet should be modified so as to contain more bread and meat, and also vegetables and small quantities of coffee, vinegar, and salt, somewhat as in the

Daily Ration of the United States Soldier.

Bread or flour	22 ounces.
Fresh or salt beef	20 "
Pork or bacon	12 "
Potatoes (three times a week)	16 "
Rice	1.6 "
Coffee (or tea 0.24 oz.)	1.6 "
Sugar	2.4 "
Beans	0.64 gill.
Vinegar	0.32 "
Salt	0.16 "

In concluding this general account of the subject of food, it may be stated that the effects of cooking food are three : First, to make it more palatable ; second, to utilize it thoroughly ; third, to improve its digestibility. Food which is agreeable to the taste is eaten with more relish ; and, therefore, better digested than if unpalatable. If the food were not cooked, much of it would be unfit to eat and wasted, and even if it could be eaten much would be undigested.

Hunger and Thirst.—The effects of withholding food entirely or of giving it in too small quantities are seen in cases of starvation and inanition. As an illustration of how life depends upon waste, and of the manner and relative quantities in which the tissues are destroyed to maintain life, the records of death from want of food, solid and liquid, become of interest to the physiologist. For a starving man is living upon himself, and as nature is always economical in her expenditures, one may feel sure that the very best disposition possible under such circumstances is made of the material available in maintaining life. In the wasting away that takes place in these cases we have a guide as to the character of the nourishment that the system would have taken had food been supplied from without instead of from within, and can so deduce some conclusions as to the use of food generally.

Shipwrecks, prolonged sieges, imprisonments, forced marches, etc., furnish the data by which some idea may be obtained of the state of nutrition and of the agonies and horrors in cases of death from starvation. Among the symptoms of starvation may be mentioned, first, severe pain in the epigastrium, which usually passes away in a day or so, then an indescribable feeling of weakness, a sort of sinking, in the same parts is experienced. The face becomes pale and cadaverous, and there is a wild look in the eye. General emaciation follows, an offensive odor is noticed about the body, which is covered with a brownish secretion. The voice becomes weak, muscular effort is almost impossible, the intelligence can with difficulty only be aroused. Finally death takes place, usually in eight or ten days, often accompanied with mania and convulsions.

On post-mortem examination the most striking facts usually noticed are the diminution in the weight of the body, almost entire absence of fat and blood, and the loss in bulk of the most important viscera. The coats of the intestine are so thinned as to be almost transparent, the gall-bladder is distended with bile, and decomposition sets in very rapidly.

Death from inanition or insufficient food, though more prolonged than that from actual starvation, is essentially the same process only slower, being characterized by the same symptoms, and the same post-mortem changes. Many babies and young children in large cities and even in the country die from inanition—actually starved to death, undoubtedly through ignorance in some cases ; but in

others, however, the length of time in death from inanition varying so, and being often so extended, advantage is frequently taken of this to obscure and mask the true cause of death by those interested in escaping from the penalties of their criminal neglect of the children placed in their charge.

As already observed, one of the most prominent symptoms of starvation is the loss of weight. It may be generally stated that when this loss exceeds from twenty to fifty per cent. of the weight of the body, death takes place.

Relative Loss of Tissue in Starvation in 100 Parts.

	In doves, according to Chossat.[1]	In cats, according to Voit.[2]
Fat	93.3	97
Blood	75.0	27
Spleen	71.4	67
Pancreas	64.1	17
Liver	52.0	54
Heart	44.8	3
Intestines	42.4	18
Muscles	42.3	31
Muscular coat of stomach	39.7	
Pharynx and œsophagus	34.2	
Skin	33.3	21
Kidneys	31.9	26
Respiratory apparatus	22.2	18
Osseous system	16.7	14
Eyes	10.0	
Nervous system	1.9	3

It will be observed from a glance at the results obtained by Chossat and Voit that the difference in the relative loss of the tissues is very considerable. Thus the nervous system loses only a little over one per cent., the muscles over forty per cent., while more than ninety per cent. of the fat disappears.

Now it has been noticed that in starvation the temperature falls, and most rapidly as death approaches; this is so evident that the immediate cause of death is undoubtedly cold. When it is remembered that one of the principal uses of the fatty principles is to produce heat through their combustion, the large loss of fat in such cases becomes intelligible, the animal using up its own fat as so much fuel.

Inasmuch as no food has been introduced into the body there is nothing for the economy to make blood out of, hence the small quantity found in the body after death from starvation. Further, what there is of it is of the most inferior quality, rather injurious than otherwise; for through the impeded circulation the worn-out and effete matters which are excreted and carried out of the system so rapidly in health accumulate in the stagnating inspissated fluid and represent so much poison.

[1] Recherches Experimentales sur l'Inanition, p. 92. Paris, 1843.
[2] Hermann: Physiologie, Band vi., s. 97.

Even though one should recover from the effects of long deprivation of food, the system for weeks afterward remains in a condition peculiarly favorable to the reception of any zymotic poison. Hence, from time immemorial, famine has been the harbinger, the forerunner of epidemics, the plague, etc. Almost invariably after a long siege, where there has been insufficient food, unless careful measures are taken, disease breaks out and carries off many of those spared by the sword. In the often quoted words of Chossat, "inanition is a cause of death which advances in the front and in silence in every disease in which alimentation is not in a normal condition."

Terrible as the pangs of hunger are, those of thirst are worse. Man and animals will live longer without solid food than when deprived of water, man dying usually in a few days when no water at all has been taken. When it is remembered that about three-fifths of the body consists of water this is readily accounted for.

The sensation of thirst, though caused by this general want of the system for water, is referred to the mouth and throat, which are first sensibly affected. These parts become very dry and hot and there is an agonizing feeling of constriction, fever sets in, the blood is very much diminished in quantity and becomes thickened, the urine is scanty and burns, the viscera may be said to be almost inflamed, delirium generally precedes death.

The importance of giving water freely, internally and externally, in health and disease cannot be too much insisted upon. No detailed argument is necessary to prove this point. The simple fact that within four days even, men have died when entirely deprived of water speaks for itself.

It will be remembered that the proteids, carbohydrates, fats of the food, being more or less oxidized in the economy, liberate energy. Of the energy so set free the greater part, as we shall see hereafter, disappears as heat, the remaining part as muscular or other form of vital energy, the temperature of the body remaining practically constant.

Use of Food.—The use of food then is to repair not only the waste of the tissues, but also to supply the fuel for the production of energy. In the child, however, the food not only supplies these two wants, but also furnishes the materials for its growth, hence the large and constant amounts of food demanded by an active, healthy child.

Again, the food of the female during gestation must furnish the materials out of which the child is developed, as well as supply her own wants. The food, under these circumstances, ought to be most generous, both in quantity and quality, that neither mother nor child should suffer.

Striking contrasts are offered, according to the particular use made of the food in one or more of the ways just mentioned by different classes of living beings, or of an animal at different periods

of its existence. Thus in trees, making no muscular or nervous effort and, therefore, wasting but little, all their food can be applied to increase their size, hence their indefinite growth. Insects, on the contrary, being most active, are usually small animals, the greater portion of their food being used up in producing their various actions, and little left for growth. In the fœtal state of man the food is applied to growth, in the adult for the repair of the tissue and the production of energy, hence a man cannot grow indefinitely, there being no food available for growth. Inasmuch as the quantity of food that can be taken by an animal is limited by the capacity of its alimentary canal, it might be inferred, *à priori*, that if the greater part of the food is applied to one particular use, there will be little or none left for any other.

Hot-blooded animals require more food than cold-blooded ones, their more active life demanding a greater expenditure of energy. Thus a man eats usually three times a day, a boa constrictor once in three or four months. When hot-blooded animals, however, hibernate—that is, sleep for months at a time—they pass into a sort of cold-blooded state, take no food, and exist by living upon themselves. Such animals always weigh less at the end of their sleep than at its beginning; the loss of weight being, however, comparatively small, as they live so quietly during the hibernating period.

By bearing in mind these facts it becomes intelligible how individuals have been able to sustain life without taking food, water excepted, for many days beyond the period when ordinarily death from starvation ensues. By taking little or no exercise, in passing most of the time in sleep, and residing in a tropical climate, or in a temperate one during the hottest summer months, while the experiment lasts, it is evident that the system needs but little food, the waste of the tissues being reduced to a minimum, and there being but little need for heat production, on account of the high temperature of the surroundings. By living in this way, man can transform himself almost into a cold-blooded or hot-blooded hibernating animal. Under such circumstances he lives upon himself, and continually loses weight. When, as regards this loss of weight, a certain limit is reached, which varies according to the condition, previous mode of life, and peculiarities of the individual, he will certainly die of starvation unless food be taken, death from starvation being only a question of time if the system be deprived of food.

There are a number of substances which, although they can not be regarded as foods in the sense of being essential to health, are, nevertheless, consumed in such large quantities by the majority of mankind that some reference at least should be made to them in this connection. We refer to tea, coffee, tobacco, distilled and fermented liquors.

Tea and Coffee.—As the composition of tea and coffee are the same, they may be conveniently studied together. Tea is obtained

from the leaves of the Thea chinensis, coffee from the Caffea arabica, the tea and coffee plants respectively. Tea and coffee, while containing food stuffs such as sugar, gum, tannic acid, fats, salts of iron, potash, and soda, owe their peculiar properties to theïn or caffeïn. The latter is regarded now as an alkaloid, being chemically trimethyl xanthin ($C_5H_{10}N_4O_2 + H_2O$) which has been recently prepared artificially from xanthin. Dimethyl xanthin is the active principle of chocolate. The effects of tea and coffee upon the mind are well known, wakefulness, clearness and activity of thought, disposition for mental or muscular exertion, a sense of ease in respiration, and general comfort. The exhaustion and nervousness often following the excessive use of tea appears to be due to the loss of sleep rather than to any poisonous action of its alkaloid. As regards nutrition, tea and coffee do not appear so much to supply the economy with nutritive material as to promote the transformation of that already taken, the exhalation of carbon dioxide being increased.[1] As theïn and caffeïn exist in tea and coffee only to the amount of 6 per cent. and $\frac{1}{3}$ per cent., respectively, a cup of tea would contain only about 1.2 grammes (20 grains) of theïn and a cup of coffee 0.05 grammes (0.7 grain) of caffeïn, as the remarkable effects of tea and coffee upon the system are not proportional, therefore, to the amount of the active principle that they contain, the action of the latter in the economy would appear to resemble that of a ferment, the food and tissue being transformed and carbon dioxide set free as in the various fermentations induced by yeast.

Tobacco.—As the employment of tobacco is most extensive in all classes of society, a few words on its effect upon the system in this connection appear appropriate. The active principle of tobacco is a poisonous alkaloid, nicotia, consisting of $C_{10}H_{14}N_2$. Experiments appear to show that while the use of tobacco increases the elimination of uric and phosphoric acids the feces and urine themselves are diminished, the exhalation of carbon dioxide being but little affected. While the excessive use of tobacco no doubt produces a state of wakefulness, trembling, and nervous excitement, it cannot be denied that when moderately used it is often very beneficial, quieting and soothing the nervous system when exhausted by bodily and mental effort, and even in ordinary circumstances producing a general tranquillizing effect.

Tobacco seems also to promote digestion, stimulating the secretion of the gastric juice by reflex action, hence the common custom of smoking a cigar after breakfast or dinner.

Alcohol.—Before considering the use of wines, malt liquors, and spirits, it is necessary to learn, if possible, the effects of pure alcohol upon the human body, since this principle is contained in large or small quantities in all such fluids. Alcohol chemically consists of CH_3CH_2OH, and the first question to be investigated is, what be-

[1] Smith, Philosophical Transactions, Vol. 149, 1859, p. 681.

comes of it when taken into the system? According to some experimenters, very little alcohol is found in the excretions, 95 per cent. appearing to be oxidized, burnt up; according to others, however, alcohol is found in the ventricles of the brain unchanged, and is eliminated by the lungs, skin, and kidneys.

It appears, therefore, that alcohol may be consumed in the economy, or excreted as such, or partly oxidized and partly excreted. In either case, however, alcohol can be of no benefit to the system, for if it is found as such untransformed in the organs or excreted unchanged, it cannot supply any want, simply passing through the system, and if it is burnt up it must interfere with the oxidation of other substances, such as fat, etc., which under ordinary circumstances would, through combustion, disappear. If the latter view be correct, we have an explanation of hard drinkers becoming often so fat, the alcohol being burnt in preference to their fat, and so allowing their fat to accumulate in the muscles, in the liver, heart, etc., or, what is more likely, the alcohol in some way interferes with that splitting of food or tissue that normally precedes its oxidation.

Alcohol can never substitute the natural drink of man, water. Many substances which are soluble in the latter are precipitated by the former, and, hence, useless to the system; further, it does not supply any principle to the tissues.

Alcohol, in diminishing the amount of urea excreted and the action of the skin, and in interfering with natural combustion, perverts the whole nutrition of the body. The active changes and the rapid removal of the effete matters, so characteristic of healthy life, are retarded by alcohol; hence the susceptibility of the dram drinker to zymotic poisoning and chronic disease. It is well known, also, that less food is taken when alcohol is used, and so alimentation is affected. It is often urged that alcohol "keeps the cold out," but as the cutaneous vessels dilate under the use of alcohol through paralysis of the vaso-constrictor nerves, more blood, and therefore more heat, comes to the surface, which instead of being retained within the body as it would otherwise be, escapes, the natural effect of the cold being to contract the vessels and of so keeping the heat in the body. Whether this be the true explanation or not, the fact remains the same, that Arctic voyagers keep the cold out far better without the use of alcohol than with it. Finally, in addition to these facts, when it is remembered that many persons preserve their mental and bodily health perfectly without ever touching alcohol, it is difficult to offer a single good physiological reason for the use of alcohol at any time, the body being in health.

It must not be forgotten, however, that almost every people, savage or civilized, use alcohol in some form or another. Whether some, as yet unknown, want is supplied to the system by alcohol, or whether it is used merely to drown sorrow or to relieve ennui, is an

undecided question.[1] Among civilized people life is so artificial and man is so harassed bodily and mentally that, unfortunately, perfect health is far from being common. Life at times becomes weary, the heart feels oppressed, digestion is sluggish, the circulation impeded, muscular languor is present; then alcohol is useful, for it is a nervo-muscular stimulant. The action of the heart is accelerated, the blood flows more rapidly, the heart is relieved, and good results from its use. As a medicine, alcohol is indispensable; when used for any other purpose, little or nothing can be said in its favor.

Liquors, Distilled Liquors, Wines, Malt Liquors.—Liquors are prepared by treating dilute alcohol with sugars, ethereal oils, and aromatics. The distilled liquors most commonly used are brandy, whiskey, gin, and rum. They contain, as a rule, a little more than 50 per cent. of alcohol, and hence, when abused, their bad effects. Brandy, the most valuable of them as a medicine, is obtained by the distillation of wine; whiskey from rye, wheat, etc.; gin from different grains rectified by juniper, and rum from molasses. Brandy, whiskey, and gin diminish the amount of carbon dioxide exhaled, and so interfere with vital processes. Rum, however, increases the carbon dioxide exhaled, and, therefore, is less hurtful in its effects. It has long been known that the rum drinker lives longer than the brandy or gin drinker.

Wine, or the fermented juice of the grape, is called full-bodied or light, according to the amount of alcohol present. There is always less alcohol in wines than in the distilled liquors just mentioned; thus port, Madeira, and sherry contain from 15 to 20 per cent. of alcohol; claret, sauterne, hock, about 10 to 15 per cent. In countries where the light wines are used by all classes of society, the horrible effects of spirituous liquors are almost unknown, the per cent. of alcohol being so small in light wines.

Wine contains, in addition to alcohol, sugar, gluten, and a number of salts, etc. Wine is nutritious in proportion to the amount in which these substances are present. In the preparation of many wines, like champagne, the amount of carbon dioxide is increased; hence, their great use as diffusible stimulants in those cases where the vital powers demand prompt and active stimulation. Under such circumstances there is no better medicine than champagne.

Beer, ale, and porter are made from malted barley with the addition of hops, the fluid remaining after separation of nitrogenous matters being treated with yeast. All malt liquors contain alcohol; about 1 to 4 per cent. in the weaker, and from 6 to 8 per cent. in the stronger kinds. Even as much as 12 per cent. is found in the heavy English beers.

[1] Important researches have been made recently by Chittenden (The American Journal of the Medical Sciences, April, 1896) upon the effect of alcohol upon the various digestive secretions. However valuable, such investigations will not throw any light upon the effect of alcohol upon the system until supplemented by a knowledge of the effect of alcohol upon the processes of secretion, absorption, etc.

Composition of French Beer.[1]

Water	947.00
Alcohol	4.50
Dextrin, glucose, etc.	41.40
Nitrogenized substances	5.26
Mineral salts	1.84
Bitter principle not determined.	
	1000.00

A most noticeable feature in the composition of French beer as just given is the small amount of alcohol, and the very large quantity of glucose, etc. There are also nitrogenized substances, mineral salts, and a bitter principle. Apart from the alcohol they contain, malt liquors are nutritious on account of these carbohydrate and nitrogenized and inorganic principles. They are often of great service to persons who are run down, debilitated, or who are slowly recovering from some exhausting, low type of disease, being taken then as a medicine. In such cases the small quantity of alcohol in the malt liquor is beneficial, acting as a stimulant, the hops are useful as a tonic, and the remaining principles as food.

It will be seen from what has been said of alcohol that the evil resulting from the abuse of liquors of all kinds is proportional to the amount that is present of this principle, that malt liquors and light wines are less injurious than brandy and whiskey, and that beer, ale, etc., containing so many nutritious principles, closely approximate to the true idea of a food.

Condiments, such as mustard, pepper, and osmazome, the aromatic matter in roast meat, while not contributing to the repair of the tissue or the liberation of energy, are important adjuncts to food, stimulating the nervous system and exciting secretion. Indeed were it not for the flavor imparted to food by such substances it is doubtful whether it would be eaten for any length of time by either man or beast.

[1] Payen: Substances Alimentaires, p. 462. In the original table of Payen, 957 is given, instead of 947, probably a typographical error.

CHAPTER V.

DIGESTION.

In order that the food should fulfill its functions in the economy it must be assimilated, and before that can be accomplished the food must be first digested and then absorbed. Digestion should, therefore, be studied first.

Under the general term digestion are included several processes: the prehension of food, its mastication and insalivation, deglutition, the changes effected in the food during its passage through the stomach, the small and large intestine, and defecation.

Mastication.

The chewing of food, or mastication, is effected by the teeth, which, in the adult condition, are thirty-two in number, viz., eight incisors, four canines, eight premolars, and twelve molars. A tooth is usually described as having three parts. That portion which is seen in the mouth is called the crown. The tapering portion inserted in the socket, or alveolus of the jaw, is the root or fang, and is held in position by fibrous tissue continuous with the periosteum of the jaw and submucous tissue of the gum. The intermediate constricted part of the tooth between the crown and the fang is known as the neck, the accumulation of fibrous tissue at this position being called the dental ligament.

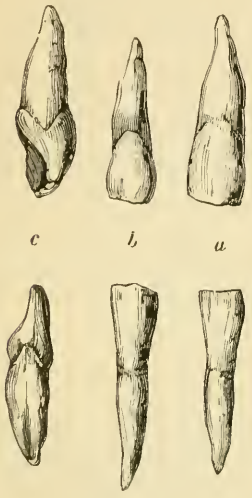
The incisor or cutting teeth (Fig. 13) four in each jaw, are nearest to the middle line in front of the jaw. They are inserted in their sockets by a single fang. The crown of the tooth is wedge-shaped, and presents a wide, sharp, and chisel-like edge, its lingual or inner surface is concave from above downward. In the upper jaw the central incisors are larger than the lateral ones, whereas, in the lower jaw the lateral are larger than the central ones. The incisors are well adapted to cut and bite the food.

The tooth next to the lateral incisors in both jaws is called the canine (Fig. 14), and corresponds to the large tearing and holding tooth in the dog, hence its name. The canine teeth, four in number, are larger than the incisor teeth. The crown is conical and bevelled behind, the fang is longer than in any of the other teeth, and laterally exhibits a slight furrow, as if indicating a tendency to subdivide into two. The upper canine or eye teeth are larger and longer than the lower ones. The latter are often called the stomach teeth. The canine teeth assist the incisors in dividing the food.

The premolars, two in each jaw (Fig. 15), succeed the canine.

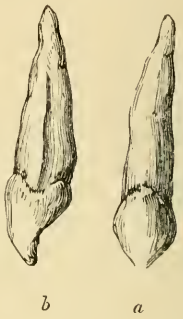
They are shorter and thicker than the latter. The crown is cuboidal, convex externally and internally, and exhibits upon the triturating surface two eminences or cusps, hence their name of bicuspids. The fang is conical and flattened, and deeply grooved. The upper premolars are larger than the lower ones, and their fang is more or less subdivided into two.

Fig. 13.



Incisor teeth of the upper and lower jaws. *a*. Front view of the upper and lower middle incisors. *b*. Front view of the upper and lower lateral incisors. *c*. Lateral view of the upper and lower middle incisors, showing the chisel shape of the crown; a groove is seen marking slightly the fang of the lower tooth. (QUAIN.)

Fig. 14.



Canine tooth of the upper jaw. *a*. Front view. *b*. Lateral view, showing the long fang grooved on the side.

The premolar teeth are succeeded by the twelve molar or grinding teeth, six in each jaw. The molar tooth (Fig. 16) has a cuboid crown. The triturating surface in the upper molars at the four angles is elevated into four tubercles, named from before backwards; externally and internally, the paracone, metacone, protocone, hypocone, a diagonal ridge, connecting usually the protocone and metacone. In the lower molars there are five tubercles or cusps, three on the outer side, the two hypoconulids and protoconulid from before backwards, two on the inner side, the entoconulid and metaconulid. The lower molars are inserted in their sockets by a pair of conical fangs, the upper ones by three fangs, two external and one internal, the latter is the largest and grooved. The first molar tooth—that is, the one most anteriorly situated—is the

Fig. 15.

First bicuspid tooth of the lower jaw. *a*. Front view. *b*. Lateral view, showing the lateral groove of the fang and the tendency in the upper to division. (QUAIN and SHARPEY.)

Fig. 16.

First molar tooth of the upper and lower jaws. They are viewed from the outer aspect. (QUAIN and SHARPEY.)

largest, the third, or the wisdom tooth, the smallest. Often, however, in the savage races of mankind, in the milk teeth of civilized races, in the fossil man, and in the monkey, the last molar is the largest. It is by means of the molar teeth that the food is crushed and ground up.

During mastication the external tubercles of the lower molars are opposed to those of the upper ones, and through the lateral motion of the lower jaw inward, the external tubercles pass down the inclined surfaces of the external ones and up those of the internal tubercles of the upper teeth, crushing the substances between them.

The teeth are arranged in the jaw somewhat in the form of a curve. In savage races, on account of the prominence of the canine teeth, the curve is rather of an oblong form, and in civilized races the curve is often V-shaped. The incisor teeth of the upper jaw overlap those of the lower, and the external cusps of the premolars and molar teeth close outside those of the lower jaw. It will be also observed that the central incisors of the upper jaw extend over the central and half of the lateral incisors of the lower jaw, whilst the upper lateral incisors come in contact with the outer half of the lower laterals and the anterior half of the lower canines. The canine teeth of the upper jaw extend over half of the lower canines and half of the lower first premolars. The first premolar of the upper jaw is opposed to the half of the first premolar and half of the second premolar of the lower jaw, whilst the second upper premolars impinge upon the posterior half of the second premolar and anterior half of the first molar of the lower jaw. The first molar of the upper jaw is opposed to the posterior two-thirds of the first molar and anterior third of the second molar of the lower jaw. The second upper molar impinges upon the posterior third of the second and anterior third of the last molar of the lower jaw. The last molar in the upper jaw is opposed by that part of the third molar in the lower jaw which remains uncovered by the second upper molar.

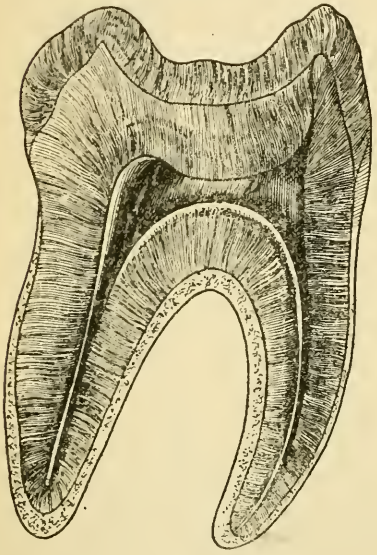
By this disposition it will be seen that no two teeth are opposed to each other only, and that, with the exception of the last molar, each tooth in the upper jaw is opposed to two teeth in the lower one. If a tooth is lost, or even two alternate ones, the remaining teeth will therefore be still useful.

If the teeth of man be compared with those of a carnivorous animal, like a lion, or with those of a herbivorous one, like a rhinoceros, it will be found that in man the teeth are both of the carnivorous and herbivorous kinds, and pretty evenly developed, whereas, in the lion, on the one hand, the teeth are all of the biting, cutting, and tearing character; while in the rhinoceros, on the other, the largest teeth are of the grinding and crushing character.

On making a longitudinal section of a tooth, of a molar for ex-

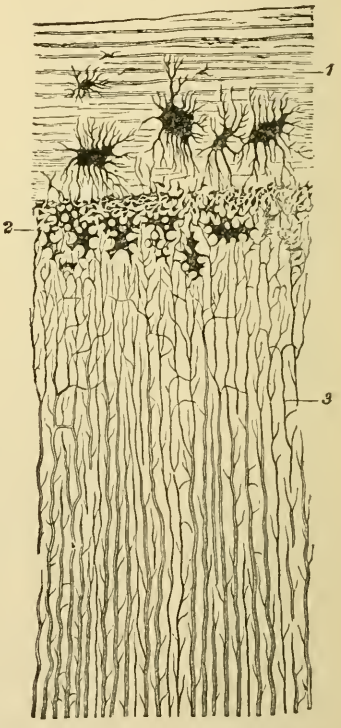
ample (Fig. 17), it will be observed that there is a cavity within the crown of the tooth which extends into and through the fangs opening by a small aperture at their apices. This space is the pulp cavity, and contains, in the living tooth, the pulp. The tooth will be also seen, from such a section, to consist of three parts, dentine, or ivory, a yellowish-white substance bordering the pulp cavity, enamel, a harder and whitish substance capping the crown, cement, a translucent bony-like layer encrusting the roots.

Fig. 17.



Section of human molar tooth magnified. (Owen.)

Fig. 18.

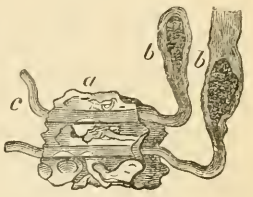


Section of fang, parallel to the dentinal tubules (human canine). Magnified 300 diameters. 1. Cement, with large bone-lacunæ and indications of lamellæ. 2. Granular layer of Purkinje (interglobular spaces). 3. Dentinal tubules. (Waldeyer.)

The dentine constitutes the great bulk of the tooth. Chemically it consists of about twenty-eight parts of animal matter (tooth cartilage), and seventy-two of earthy salts; among the latter are principally found calcium phosphate, some calcium carbonate, and magnesium phosphate. When examined with the microscope dentine (Fig. 18) is seen to consist of an amorphous translucent matrix, in which are imbedded numerous canals or tubes, whose walls are distinct from the matrix. These latter are the dental or dentinal tubules, and average in diameter at their commencement $\frac{1}{1800}$ mm. ($\frac{1}{45000}$ of an inch). The intermediate space between the adjacent tubules is about three times their diameter. The dental tubules open at their inner ends or beginnings into the pulp cavity, outwardly they pass to the periphery of the tooth. The tubules run generally in a parallel, but

somewhat wavy course. As they pass outward they become gradually narrower, dividing and subdividing, giving off innumerable small branches, which anastomose or end blindly. Some of the terminal branches pass into the canaliculæ of the cement, others into the so-called interglobular spaces, irregular cell-like cavities in the matrix. The walls of the dental tubules are about as thick as their calibre. In the living tooth the dental tubules are filled with the dental fibers, which are prolongations from the odontoblastic cells of the pulp (Fig. 19). These dental fibers are possibly the terminal filaments of the nerves supplying the tooth. The contour markings observed in the teeth are due to irregularities in the matrix or intertubular substance.

Fig. 19.



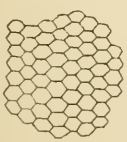
a. Dentine. *b*. Odontoblastic cells. *c*. Fibers. (Tomes.)

As age advances there is deposited upon the inner surface of the dentine a secondary kind of dentine, known as osteo-dentine, which resembles both dentine and bone. This appears to be due to a sort of ossification of the pulp, the effect of which is gradually to obliterate the latter and the pulp cavity.

Enamel.—The crown of the tooth is covered with the enamel, the hardest of organic substances. It is, however, gradually worn down by protracted use. The enamel is thickest upon that part of the tooth most used in trituration, here it exists in several layers; it is thinnest at the roots, where it gradually disappears.

Chemically, enamel consists of about five parts of animal matter, and ninety-five of earthy constituents, the latter being mostly calcium phosphate. Microscopically, enamel consists of solid six-sided prisms, the enamel fibers having an average diameter of $\frac{1}{2000}$ mm. ($\frac{1}{5000}$ of an inch) and a length of $\frac{1}{40}$ mm. ($\frac{1}{1000}$ of an inch). Each prism rests by its inner end upon the dentine, the outer end being covered with the cuticle of the teeth. Usually there are several layers of enamel prisms, the outer layer being then covered with the cuticle. The prisms, while arranged in a parallel manner, do not run in an exactly straight direction, the course being rather an undulating one. The prisms, when viewed horizontally from their outer ends, present a tessellated appearance (Fig. 20). The so-called cuticle of the teeth, or membrane of Nasmyth, just referred to as covering the outer ends of the enamel prisms or fibers, averages about the $\frac{1}{6000}$ mm. to the $\frac{1}{12000}$ mm. ($\frac{1}{15000}$ to the $\frac{1}{30000}$ of an inch) in thickness. It acts as a protective covering to the enamel. By some histologists the cuticle of the teeth is regarded as a very thin cement.

Fig. 20.



Section of enamel, highly magnified, at right angles to the course of its columns; exhibiting the six-sided character of the latter. (Leidy.)

Cement.—The crusta petrosa, or cement, covers the roots of the teeth, beginning at the neck as a thin layer and becoming gradually thicker at the fangs. It adheres very closely to the dentine and to the periosteal lining of the alveoli. Cement differs from bone in its lacunæ being more variable in their form and size, and their canicula being larger and more numerous. In many animals, like the cat, dog, and hog, the dentine, cement, and enamel are disposed as in man. In the grinding teeth of the herbivora, however, as in those of the elephant, horse, the dentine, enamel, and cement alternate with each other in such a way that as the teeth are worn an uneven triturating surface is always maintained.

Tooth Pulp.—The pulp of the tooth situated in the pulp cavity is not only the formative organ of the tooth, but the source of its vascular and nervous supply; the tooth-pulp consisting of cells, blood vessels, nerves, and a small quantity of connective tissue.

The cells are most numerous on the surface of the pulp. In this position they are known as odontoblasts and the layers formed by them as the membrana eboris. The odontoblastic cells exhibit three kinds of processes: Those passing internally into the pulp, others which serve to connect adjacent cells, and those already referred to as being prolonged into the dentinal tubules. The blood vessels pass in and out by the openings in the apex of the tooth, forming beneath the odontoblastic layer a capillary network. The nerves enter by the fang of the tooth and after giving off a few branches form a plexus beneath the odontoblastic layer. The exact manner, however, in which the nerves terminate in the teeth is not known, unless, as already mentioned, the dental fibers are of a nervous character. The teeth of the upper jaw are supplied by branches from the superior maxillary nerve, those of the lower by the inferior maxillary.

No lymphatics, as yet, have been found in the tooth pulp, or in other parts of the teeth. As age advances, the pulp of the tooth diminishes in size through its gradual calcification, the odontoblastic layer atrophies, the connective tissue increases, the capillary network disappears, the nerves exhibit a fatty degeneration, and the pulp ultimately becomes a dried-up, insensitive mass.

Although the pulp may lose entirely its vitality, yet the enamel and dentine may remain serviceable, they appearing to be perfected structures. These are, however, never reproduced when destroyed by wear or decay or by loss of the tooth, with the rare exception of where a tooth is reproduced for the third time.

The way in which the teeth are developed and the manner in which the permanent teeth are preceded by the deciduous or milk set, will be considered under the subject of reproduction.

Maxillary Bones.—The teeth in man and mammalia are confined to the maxillary bones, in which they are imbedded, the bone being moulded so to speak, around the roots of the teeth after these are developed and so forming the sockets. Between the jaw and the

tooth there is a space which in the living tooth is filled up by the alveodental periosteum. Through the elasticity of this root membrane the tooth possesses a certain amount of motion. Were the teeth immovably fixed in their sockets some shock would be felt during mastication. This alveodental periosteum, which passes imperceptibly into the gum and periosteum, consists of connective tissue in which are found nerves and vessels. There is also no sharp line of demarcation between the gum and the mucous membrane of the mouth on the one hand and the periosteum on the other.

Of the maxillary bones the superior, from being immovably articulated with the other bones of the head, are only passive in mastication. The upper teeth, however, offer fixed surfaces, against which those of the lower jaw are brought into apposition.

Intermaxillary Bone.—If the inner surface of the superior maxillary bone be examined between the middle line and alveolar margin, in most instances a suture will be readily recognized running downward and outward from the anterior palatine foramen to the outer margin of the second incisor tooth. This suture is interesting from several points of view, among others, as indicating in the embryo the distinction existing between the true superior maxillary bones and the intermaxillary bones, the latter being characterized by carrying the incisor teeth. As development advances, however, in man and to a great extent also in monkeys, the superior maxillaries coalesce to such an extent with the intermaxillaries that the primitive distinction between the bones is almost entirely lost, in some instances the suture itself even disappearing. In the other mammalia, however, the intermaxillaries remain quite distinct from the superior maxillaries and each other, and are readily disarticulated. It was this latter circumstance that led Goethe,[1] equally great as a poet and naturalist, to look for and discover the intermaxillary bone in man, so convinced was he that the skull consisted of the same bones in all the mammalia.

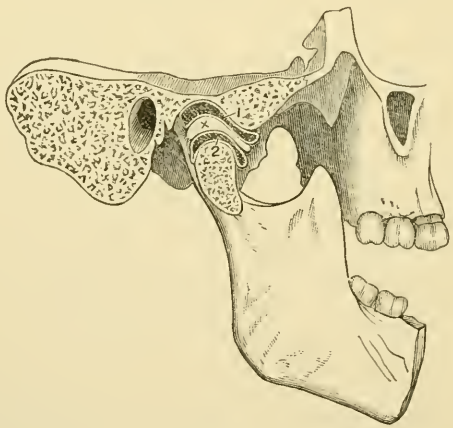
Temporo-Maxillary Articulation.—The inferior maxillary bone, mandible or lower jaw, consists in the adult of a single piece movably articulated with the temporal bone (Fig. 21). This articulation is really a double joint, since there is interposed between the condyle and the glenoid cavity a biconcave oblong piece of fibrocartilage to the edges of which is attached the capsular ligament. The spaces on either side of the cartilage are lined with synovial membrane, and there is no connection between the two cavities unless the cartilage is perforated. When the jaw is simply depressed, the joint acts as a hinge. Through the movement of the condyle on the eminentia articularis, the forward and lateral motions of the jaw are affected. The mechanism of the temporomaxillary articulation is therefore such as to insure great freedom of motion to the lower jaw. The lateral, forward, and depressing

[1] Sammtliche Werke, Band vi., Osteologie, s. 65.

actions of the jaw either succeed each other or are variously combined during the mastication of food.

If the condyle of the jaw in a carnivorous animal be examined, in a tiger, for example, it will be noticed that its long diameter is transverse, and that the glenoid cavity is grooved, hollowed out, so as to receive it. This disposition is carried out to such an extent in the badger that the lower jaw will remain depressed, interlocked, within the glenoid cavity, even though all the ligaments be cut away. The motion of the lower jaw in many of the carnivora is almost exclusively of an up and down character, there being little or no lateral motion. In the herbivora, however, as in the sheep, rhinoceros, etc., it is the lateral motion of the lower jaw that is evident in chewing. In such animals the glenoid cavity is rather shallow and the condyle oblong or ovate. The motion of the jaw in the

Fig. 21.



Antero-posterior section of the temporo-maxillary articulation of the right side. (A. T.)⅓. (Quain.)

rodentia differs from that observed both in the carnivora and herbivora, being backward and forward, like that seen in the gnawing action of a rat. This motion is rendered possible in such animals through the long diameter of the condyle and the glenoid cavity having an antero-posterior direction, as in the capybara.

The temporo-maxillary articulation combines in man, as we have seen, to a great extent, in one joint, the peculiarities just noticed in the temporo-maxillary articulation of the carnivora, herbivora, and rodent types of the mammalia.

The various movements of the lower jaw are effected by a number of different muscles: to the consideration of these let us now turn.

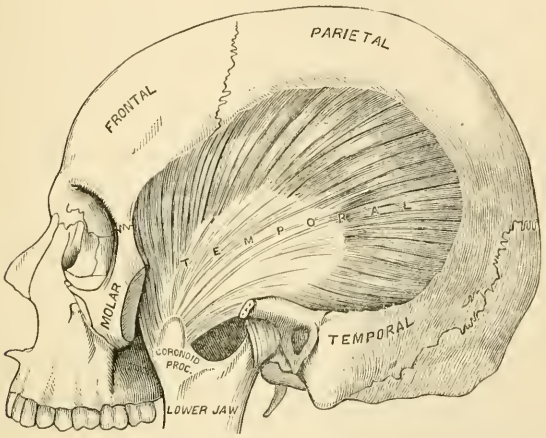
Muscles of Mastication.—These muscles naturally divide themselves into two groups, one of which elevates the lower jaw, moves it laterally or in an antero-posterior direction; the other depresses it. Let us study the former group first.

PRINCIPAL MUSCLES OF MASTICATION.

Elevators, etc.	Depressors.
Temporal.	Digastric.
Masseter.	Mylo-hyoid.
External } pterygoid.	Genio hyoid.
Internal }	Platysma myoides.

The action of the muscles becomes quite apparent when their anatomy is understood. The temporal (Fig. 22) arising from the

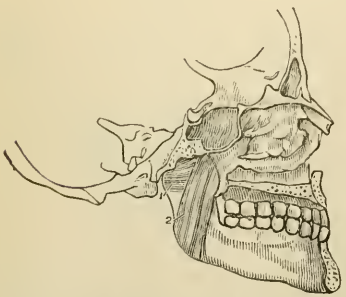
FIG. 22.



The temporal muscle, the zygoma and masseter having been removed. (GRAY.)

temporal fossa and inserted into the coronoid process raises the lower jaw against the upper. The action of the temporal is aided by the contraction of the masseter and internal pterygoid, the former muscle (Fig. 27) arising from the zygomatic arch and passing backward into the lower border of the jaw, the latter (Fig. 23) having its origin in the pterygoid fossa and its insertion in the lower and back part of the inner side of the jaw. The action of these

FIG. 23.



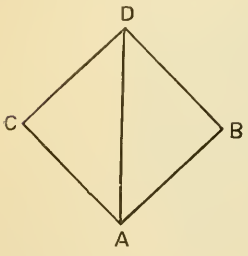
View of the pterygoid muscle from the outer side. ¼. 1. External pterygoid. 2. Internal pterygoid. (QUAIN.)

FIG. 24.

View of the pterygoid muscle from the inner side. ¼. 1. External pterygoid. 2. Internal pterygoid. (QUAIN.)

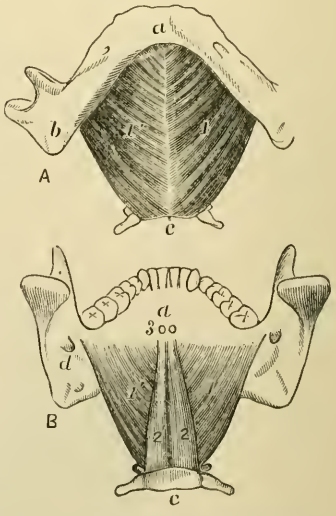
muscles is well seen in the carnivora, in which they are very large. The maximum effect of the masseter can also be well observed in the rodentia, the muscle being enormously developed in these animals. The lateral and forward motion of the lower jaw is due to the action of the external pterygoid. This muscle (Fig. 24) arises from the sphenoid, palate, and superior maxillary bones and passing backward and outward is inserted into the neck of the condyle of the lower jaw and into the inter-articular fibro-cartilage. If the condyle of the jaw on one side, the left for example, be fixed, it will be seen from the direction of the fibers of the external pterygoid that if the muscle of the opposite side contracts it will draw the lower jaw forward and laterally in an inward direction, the condyle playing upon the articular eminence, the cartilage being interposed, it having been also drawn forward by the muscle. This alternate lateral motion of the lower jaw is very evident in the chewing of the food, particularly well seen in the herbivora, in which order the external pterygoid muscle is relatively much developed. If the external pterygoid, however, act together, the lower jaw is drawn forward along the diagonal A D of the parallelogram, the two sides of which, A B A C (Fig. 25), are the directions taken by the jaw when alternately acted upon by the external pterygoids.

Fig. 25.



As regards the second group of the masticatory muscles there can be no doubt as to the function of the mylo-hyoid (Fig. 26), genio-hyoid, and platysma myoides muscles. The two former muscles passing from the hyoid bone to the mylo-hyoid ridge and genial tubercle of the lower jaw respectively will depress the jaw when the hyoid bone is fixed. The same effect is produced by the platysma, it being partly inserted into the lower border of the jaw. The action of the digastric muscle is not so simple as that of the other depressors.

Fig. 26.



A. The lower jaw and hyoid bone, from below, with the mylo-hyoid muscles attached. B. The same from behind, with the mylo-hyoid and genio-hyoid muscles attached. (A. T.) 1/3.

The digastric muscle, as its name implies, is double-bellied, consisting of an anterior and posterior muscular part with an intervening tendinous portion. The tendon often passes through the stylo-hyoid muscle, gliding through a small synovial bursa,

and is connected with the body and great cornu of the os hyoides by a broad band of aponeurotic fibers in the form of a loop and lined with synovial membrane. The posterior belly of the digastric muscle passes upward, backward, and outward from the tendon to the digastric groove of the temporal bone, the anterior belly upward and forward to the inner surface of the jaw, near the symphysis. An interesting fact to be noticed is that the anterior belly is supplied by the mylo-hyoid branch of the inferior maxillary branch of the fifth nerve, the posterior belly by the facial, as we shall see when we come to study the nervous system; this shows that the muscle is essentially a double one.

Such being the disposition of the digastric muscle, it follows that if the jaw be fixed and the anterior belly alone contracts, the hyoid bone will be elevated anteriorly, as it is by the genio-hyoid and mylo-hyoid muscles in the first stage of deglutition. If, however, the posterior belly alone contracts, the hyoid bone will be raised upward and backward, its action being similar to that of the stylo-hyoid muscle. Should both bellies contract, then the hyoid bone will be elevated almost perpendicularly. On the other hand, should the hyoid bone be fixed by its depressor muscles, the lower jaw will be slightly depressed if the anterior belly of the digastric muscle acts alone; should the posterior belly act independently, then the mastoid process will be drawn downward, and with it the back of the head, thereby elevating the upper jaw and opening slightly the mouth. This action of the posterior belly alone, or with the anterior one acting with it, is no doubt aided by the deep muscles of the neck. While it is possible that the lower jaw can be depressed by the anterior belly of the digastric acting alone, it is most probable that the posterior belly acts with the anterior one in producing this effect, the muscle acting in the reverse direction of that just referred to producing the movement of the back of the head. This view is confirmed by the fact that in several animals, in the orang, for example, as observed by the author,[1] the posterior belly of the digastric muscle is alone present and inserted into the angle of the jaw. That the mouth is to a certain extent opened by the elevation of the upper jaw through the backward motion of the head due to the contraction of the posterior belly of the digastric and of the muscles of the neck, may be shown in various ways. For example, when the chin is placed upon a table, the lower jaw being then immovable, or when the lower jaw is firmly fixed, as in certain surgical operations, it will be observed that the mouth can be slightly opened, though the lower jaw cannot be depressed.

It must be admitted, however, that the movement of the upper jaw in this respect has not much significance, as the opening of the mouth is essentially due to the depression of the lower jaw.

Résumé.—The effect of mastication is that the solid food taken into the mouth is cut and crushed and ground up by the teeth.

[1] H. C. Chapman, Proc. Acad. of Nat. Sciences, 1880, p. 161.

The little pieces that ooze out between the teeth and the cheeks are pushed under the teeth again by the muscular action of the cheeks and lips, while the fragments that escape within the inner side of the teeth are forced back by the tongue. The importance in man of the action of the cheeks, lips, and tongue in mastication is well seen when there is a paralysis of the facial or hypoglossal nerves. In such cases the food accumulates between the cheeks and the teeth, and the want of action of the tongue is seen both in the difficulty of mastication and deglutition. The same effect can be produced by cutting the corresponding nerves in animals.[1] The thorough mastication of the food insures its further digestion. Indeed, a most fertile source of dyspepsia is the too common custom of bolting the food. In the latter part of the last century it was shown by Spallanzani[2] that different kinds of meat when enclosed in perforated tubes and so swallowed, passed through his alimentary canal comparatively undigested. When the meats, however, were first broken up and then placed within the tubes very little undigested matter was found in them when passed by the anus.

In grammivorous birds, like the common fowl, for example, the want of teeth is supplied by pebbles swallowed with the food, the gizzard triturating the food by means of the pebbles.

Mastication should be kept up until the food is thoroughly ground up. The teeth are so exquisitely sensible to the presence of any hard matter that we are enabled by them to know at once whether the process of mastication is completed. During mastication not only is the food thoroughly triturated, but it becomes gradually incorporated with the saliva. To the consideration of the production and effects of this secretion let us now turn.

[1] Panizza, Gaz. Méd., 1835, p. 419.
[2] Fisica Animale et Vegetabile. Venezia, 1782, Tomo secondo, p. 52.

CHAPTER VI.

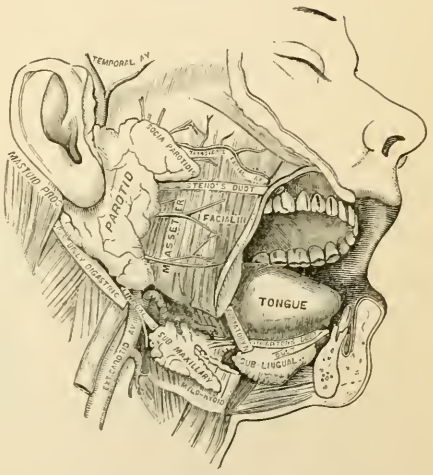
DIGESTION.—(*Continued.*)

INSALIVATION AND DEGLUTITION.

Insalivation.

The saliva consists of a mixture of the secretion of the parotid, submaxillary, and sublingual glands, usually known as the salivary glands (Fig. 27), and also of the labial, buccal, lingual, molar, and pharyngeal glands. The salivary glands are regarded at present by histologists as being compound tubular rather than racemose or grape-like glands as was formerly supposed, the secreting power residing in the cells with which the diverticula of the ducts are lined. According to recent researches[1] the lumen of the ducts appears to be prolonged as a capillary network extending between and even into the secreting cells.

Fig. 27.



The salivary glands. (Gray.)

Let us consider now the properties of the saliva secreted by these different glands beginning with the parotid, which is secreted more abundantly than that of the other glands. The parotid saliva as obtained from salivary fistulæ or by introducing a tube directly into the duct of Steno, is an alkaline, clear, watery fluid, the latter property enabling it to readily mix with and soften the food. The flow of the parotid saliva is most active during mastication, about three times as much saliva being secreted on the masticating side of the mouth as on the opposite one. These facts, taken into consideration with that of the orifice of the duct of Steno being opposite the second molar tooth, so situated that the saliva at once comes in contact with the food that is being masticated, suggest the view that the function of the parotid saliva is to aid mastication.

The facts of comparative physiology confirm this conclusion. Thus, in the ruminantia, which chew their food very thoroughly,

[1] Lasertein, Pflüger's Archiv, Band 55, 1893, s. 417.

the parotid glands are very large; on the other hand they are usually absent in the cetacea, whales, dolphins, etc., and but little developed in the otter, seal, hippopotamus, the latter not needing parotid glands, the water in which they live or pass much of their time sufficiently moistening their food. It has also been shown that if the duct of Steno be divided in the horse, the time required in chewing a feed of oats is three times as much as under ordinary circumstances. The food is also swallowed with difficulty under such circumstances, through the want of its proper admixture with the saliva. It is well known also that less saliva is produced in the horse on a feed of oats than on one of hay or straw, and that food already moistened excites little if any flow of saliva.

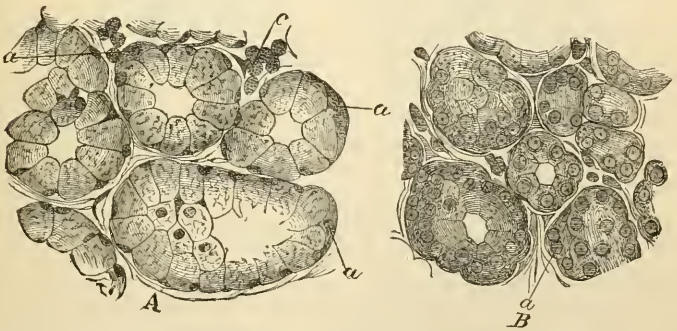
Reflection upon the relative development of the submaxillary glands in different kind of mammals in connection with their habits leads to the conclusion that the principal use at least of the submaxillary saliva is that of lubricating the food, and of so promoting its deglutition. Thus, in the carnivora in which the food is rather bolted than chewed, the submaxillary glands are large, the parotids small. In the great ant-eater, Myrmecophaga jubata, while the parotid gland is so small as to have escaped even the notice of Cuvier, the submaxillary gland is over sixteen inches in length and secretes an extremely viscid tenacious saliva which lubricates the extensible tongue to which the ants adhere and upon which the animal subsists. That the function of the submaxillary saliva in man is to lubricate the food and so aid its deglutition is shown by its viscidity as compared with the parotid saliva, its consistence being such that it coats but does not penetrate the bolus of food. Further, the submaxillary is often mixed with the sublingual saliva even before it passes into the mouth, the duct from the sublingual gland, the so-called duct of Bartholinus, not unfrequently joining the duct of Wharton or terminating with it by a common orifice. The sublingual saliva transmitted to the mouth mostly by the ducts of Rivinus is more viscid than the submaxillary saliva and promotes deglutition, therefore, even to a greater extent.

That the function of the submaxillary and sublingual saliva is essentially to aid the swallowing of the food is still further shown by the fact that the placing of a sapid substance upon the tongue immediately induces a copious flow of submaxillary saliva which is due, as we shall see hereafter, to the reflex stimulus of the chorda tympani nerve.

The fluids secreted by the labial, buccal, or molar glands, etc., have never been studied separately in man. In animals in which the ducts of the parotid, submaxillary, and sublingual glands have been ligated, the fluid still secreted by the mouth comes from the glands just mentioned, and consists of a thick, opaque, grayish mucus, containing salivary corpuscles, desquamated epithelial cells, etc. The turbidness of the mixed saliva is due to this secretion, that from the salivary glands proper being transparent.

It has been learned from the researches of Heidenhain,[1] Lavdowsky,[2] Langley,[3] and others, that the minute structure of the salivary glands differs considerably according as they are examined after a period of rest or activity, and that such differences are more marked in the so-called mucous glands, like the submaxillary, in which the secretion is viscid, mucin-like, than in the serous or albuminous ones, like the parotid, in which the secretion is limpid. Thus, if, after a period of rest, a section of a "mucous" gland—the submaxillary gland of the dog, for example—be examined, the cells of an alveolus (Fig. 28, *A*) will be found to stain with carmine more readily in certain parts than in others. The nuclei and surrounding protoplasm, and the demilune cells—apparently young cells lying next to the basement membrane—become deeply tinged, while the remaining portion of the cell remains uncolored, due apparently to its protoplasm in this situation having been converted into a mucin-like substance. If, however, similar sections of the gland be made after a period of activity induced by stimulation of the chorda tympani nerve, it will be observed (Fig. 28, *B*) that but a small portion, if indeed any part, of the cell has resisted

Fig. 28.



Section of a "mucous" gland. *A*. In a state of rest. *B*. After it has been for some time actively secreting. *a*. Demilune cells. *c*. Leucocytes lying in the interalveolar spaces. The darker shading in both figures is intended to indicate the amount of staining. (After Lavdowsky.)

coloration with carmine, and that the cells have diminished in size.

If sections of a "serous" gland—the parotid gland of a rabbit, for example—after periods of rest and activity, be treated in the same way with carmine, differences of the same kind will be observed. Thus, after rest the cells of the parotid (Fig. 29, *A*) will be found to be pale, transparent, with few granules, staining by carmine with difficulty, the nuclei irregular in outline, apparently as if shrunken. After a period of activity, on the other hand (Fig. 29, *B*), from stimulation by the sympathetic nerve, the cells will be seen to have become turbid, full of granules, staining readily

[1] Hermann, Physiologie, Funfter Band, s. 58. Leipzig, 1880.
[2] Archives of Mic. Anat., 1877, xiii., s. 281.
[3] Journal of Physiology, 1879, vol. ii., p. 260.

with carmine, the nuclei large and round, with conspicuous nucleoli, and the cells, as a whole, smaller. Such facts lead us naturally to conclude that during a period of rest the cells of the salivary glands are elaborating from the blood their characteristic secretion, the elements of the latter existing in the blood, but not the secretion itself, as such; that the secretion, as formed, is stored up (the part not staining with carmine) until needed, when at the proper moment it is forced into the interior of the gland and thence passes into the duct, the normal stimulus to the secretion being, as we shall see hereafter, impressions made upon the tongue, etc., and which are transmitted by the appropriate nerves supplying the glands. The secretion of the saliva is not a phenomenon of mere filtration due to pressure, osmosis, etc. Apart from the fact that the saliva does not exist as such in the blood it can be shown that it is excreted under a pressure greater than that exerted by the blood

FIG. 29.

Section of a "serous" gland: the parotid of the rabbit. *A*. At rest. *B*. After stimulation of the cervical sympathetic. (After HEIDENHAIN.)

of the carotid artery of the same side. Were pressure the only influence at work in the secretion of the saliva the latter would flow back to the blood rather than to the duct. Further, it is well known that during paralysis of the secretory nerves, as due to atropin poisoning, an increased flow of blood to the submaxillary gland induced by stimulation of the chorda tympani nerve will not cause secretion. Moreover, the salivary glands exhibit a kind of elective affinity in regard to the excretion of substances from the blood, salts of potassium, combinations of iodine and bromine being eliminated, but not those of iron. It is also shown that during the process of secretion, chemical action is going on, the temperature of the saliva and venous blood coming from the gland being 1.5° C. higher than that of the arterial blood supplying the gland,[1] and that the production of carbon dioxide is increased.[2] Inasmuch as during digestion, it is the mixed saliva which modifies the food, it will not be necessary to dwell especially upon the physical or chemical properties of any one particular kind of it. It may be mentioned, however, in this connection that while the parotid saliva is rich in ptyalin it contains no mucin, whereas the

[1] Ludwig and Spiess: Sitz. d. Wiener, Acad. Math. Nat. Classe, 1857, xxv., s. 548.
[2] Pflüger: Pflüger's Archiv, 1868, Band i., s. 686.

submaxillary and sublingual saliva are especially rich in mucin and are more alkaline than the parotid saliva. The saliva, as we find it in the mouth, consisting then of a mixture of all the different kinds of saliva, is an alkaline, colorless, turbid, mucilaginous, ropy fluid with a specific gravity of about 1003. While the reaction of the saliva is usually alkaline as just mentioned, it should be stated that it may be acid after meals. The turbidity of the saliva is due to the presence of the cells of the buccal epithelium, salivary corpuscles which are apparently altered leucocytes, and food residues. The ropy character of the saliva is due to its mucin which we have seen is chemically a compound proteid. Like all the digestive secretions the saliva consists largely of water, organic matter, and salts.

COMPOSITION OF HUMAN SALIVA.[1]

	In 1000 parts.
Water	994.2
Solids	5.8
Mucus and epithelium	2.2
Soluble organic matter (Ptyalin)	1.4
Potassium sulphocyanide	0.04
Salts	22.00

Judging from the composition of the ash the salts in the saliva appear to exist in the form of potassium and sodium chloride, potassium sulphate, and potassium, sodium, calcium, and magnesium phosphate. In the freshly secreted saliva there is also found carbon dioxide gas (65 to 67 per cent.), most of which existed in combination as carbonates and traces of oxygen and nitrogen. It was shown many years since[2] that hydrated starch when mixed with warm saliva was liquefied and converted into sugar. Any one can convince himself that such is the case by mixing in a test-tube a little boiled starch with his own saliva and testing for sugar. It will also be found that saliva has the same effect upon raw starch, only a longer time is required to produce it. The ordinary acceptation of what takes place in the conversion of starch into sugar by the saliva is that soluble starch is first formed and then erythro-dextrin (as shown by the red color given with iodine) which is further transformed into maltose ($C_{12}H_{22}O_{11}H_2O$), achro-dextrin, and a small quantity of glucose ($C_6H_{12}O_6$). It has been ascertained by experimenting with the different substances of which the saliva consists that it is the soluble organic matter, the ptyalin or salivary diastase, to which this transforming property is due, and that the different kinds of saliva will convert starch into sugar as well as the mixed saliva. The phenomenon appears to be one of hydrolysis and fermentation, the starch in the presence of ptyalin taking up water and then splitting into two or more substances.

[1] Hammerbacher, as quoted by Hammarsten. A Text-book of Physiological Chemistry, translated by Mandel, 1893, p. 173.

[2] Leuchs, Kastner's Archiv für Chemie, 1831, s. 105.

Ptyalin has not been obtained as yet in a sufficiently pure state to determine its chemical nature. It is regarded as an enzyme, an amylolytic ferment[1] acting by its presence (catalysis) simply on account of its specific action upon starch, one part of ptyalin transforming as much as two thousand parts of starch into sugar. Notwithstanding that the action of ptyalin is very rapid and energetic, only a very small quantity of sugar is produced in the mouth, the starch being so soon swallowed. As the starch remains, however, sufficiently long in the mouth to become thoroughly mixed with the saliva, and as the transformation into sugar continues after the starch passes into the stomach, for some time at least, sugar is produced, and can be detected in that organ. It is well known that outside of the body the action of ptyalin upon starch will be completely arrested by admixture with a very weak solution of hydrochloric acid. It has been inferred, therefore, that the conversion of starch into sugar by the saliva in the stomach will be suspended by the action of the hydrochloric acid of the gastric juice. We shall see, however, that the function of the gastric juice is not that of neutralizing the action of the saliva, but of digesting proteids. If the gastric juice secreted only suffices for the latter purpose, there will be none available for the suspension of the action of the ptyalin. Hence the amount of starch converted into sugar by the saliva in the stomach will depend upon the relative amounts of food and gastric juice present and upon the rapidity with which the food is mixed with the latter, the greatest amount of sugar being produced in the early stage of digestion. It has also been shown outside of the body (digestion in vitro) that the accumulation of the products of salivary fermentation will not only retard but finally arrest the action of ptyalin, but that with the removal of such products as by dialysis the fermentation action recommences. It is reasonable to suppose, therefore, that as the digestive products are as rapidly absorbed as produced, the action of ptyalin in the economy is long continued. The importance of the saliva as regards the transformation of starch into sugar must not, however, be exaggerated, since as we shall see the intestinal and pancreatic juices are equally efficient in this respect. It is stated that while ptyalin is present in the parotid saliva of the child at birth, it does not appear in the submaxillary saliva until two months later. The significance of the potassium sulphocyanide which is always found in the saliva in traces is not apparent. The remaining salts, while rendering the saliva alkaline, have not been shown as yet to fulfill any particular function in digestion.

The amount of saliva secreted during twenty-four hours, in man, has never been exactly determined. As the saliva is constantly being reabsorbed, a source of error in any calculation as to the amount

[1] On the Presence of the Amylolytic Ferment and its Zymogen on the Salivary Glands, by C. W. Latimer, M.D., and J. W. Warren, M.D., Journal of Experimental Medicine, Vol. II., 1897, p. 465.

secreted in a given time would be the risk of counting the same saliva, or, at least, the elements entering into its composition more than once. According to Dalton,[1] 31.1 grammes (about 480 grains) of saliva can be obtained from the mouth in twenty minutes without any artificial stimulus. The natural stimulus to the secretion of the saliva, however, is the presence of food in the mouth; indeed, the sight, or even the thought of food, in some individuals will make the mouth "water." The amount of saliva secreted will depend, therefore, on the quantity and quality of the food.

It has been estimated approximately that about 1500 grammes (3.3 lbs.) of saliva are secreted in the twenty-four hours. In concluding our account of the saliva there may be mentioned appropriately in this connection the peculiarity it possesses of attracting or entangling bubbles of air in the mass of food. The effect of this is that stomach digestion is facilitated through the easy access afforded to the gastric juice when the food comes in contact with this secretion. Moist, heavy bread is not readily acted upon by the secretions through its not being permeated with air in the manner just referred to.

While one of the uses of the saliva in man is certainly the transformation of starch into sugar, undoubtedly its most important function is that of aiding mastication and deglutition, the secretion of the parotid gland promoting specially the former function, that of the submaxillary and sublingual glands the latter, as we have seen in speaking of the secretions separately.

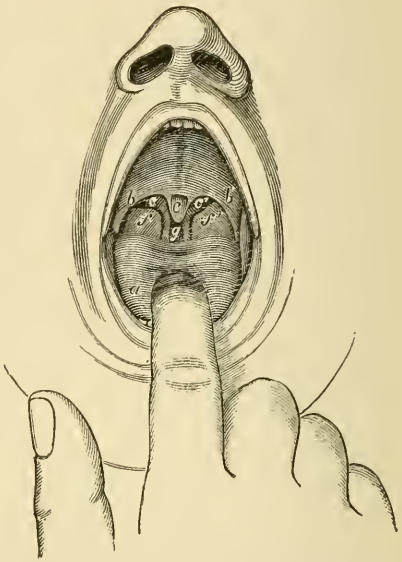
Deglutition.

After the food has been thoroughly masticated and mixed with the saliva, it is swallowed. The mouth being closed, deglutition or the act of swallowing begins by the tongue, more especially the tip, aided by the cheeks, collecting the particles of the food into a mass or bolus. Through the action of the hyoglossi muscles the tongue is then moved forward and upward, the tip, middle, and root being successively pressed against the hard palate, whereby the bolus is forced backwards through the fauces (isthmi faucium) towards the pharynx. As the bolus of food passes through the fauces, the tongue being drawn upward and backward by the contraction of the stylo-glossi muscles, and the anterior pillars of the fauces coming together, by the action of the palato-glossi muscles like two curtains, the bolus of food is thereby prevented from returning to the mouth. The importance of the tongue in deglutition may be appreciated from the fact that it is impossible to perform the act on those cases in which the tongue has been entirely amputated, is congenitally deficient, or the hypo-glossal nerve is paralyzed. In amputation of the tongue there is usually left a portion of the base sufficient to press against the palate, making

[1] Dalton, Physiology, 1882, p. 144.

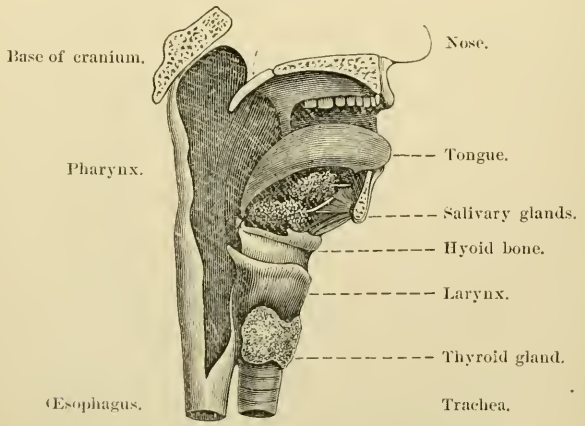
deglutition possible. At the same moment that the opening into the mouth is cut off the posterior half-arches of the fauces approach each other through the action of the palato-pharyngei muscles, the interval between them being filled by the uvula (azyzos uvulæ muscles) and the soft palate being rendered tense by the tensor palati and elevated by the levator palati the opening from the pharynx into the posterior nares is effectually closed. The importance of the latter condition is seen in cases of cleft palate or paralysis of the velum in which deglutition, at least of liquids, is impossible, the latter when swallowed returning by the nose. In the meantime the pharynx together with the larynx being elevated by the contraction of the stylo-pharyngei, stylo-hyoid, genio-hyoid, mylo-hyoid, thyro-hyoid, and digastric muscles, the latter acting more particularly through its anterior belly, the pharynx is widened and the entrance to the larynx closed, the latter being pressed up against

Fig. 30.



e. Uvula. *bb.* Anterior half arches. *cc.* Posterior half arches. *ff.* Tonsils. (Valentin.)

Fig. 31.



Vertical section of mouth and pharynx. (Milne Edwards.)

the epiglottis and the glottis itself closed by the constrictors of the larynx. That the epiglottis is indispensable in the swallowing of liquids at least is shown by the fact that in its absence "liquids go

down the wrong way," that is pass into the larynx instead of into the œsophagus. Solids, however, can be swallowed in the absence of the epiglottis, since the larynx being drawn up under the base of the tongue is sufficiently well covered by the latter to prevent food entering it. If, however, a small fragment of food, a crumb, for example, be swallowed incautiously in the absence of the epiglottis, it is very apt to pass into the larynx and give rise to a fit of coughing. At the moment of the closing of the openings of the pharynx into the mouth, nares and larynx, the mylo-hyoid muscles contract quickly and powerfully and the bolus of food is projected or shot down under high pressure through the pharynx into the œsophagus, reaching the cardiac orifice in about 0.1 second where it is usually temporarily retained. In some cases, however, owing to the cardiac orifice of the stomach being relaxed, the bolus of food passes directly into the stomach. The rapid movement just described is followed immediately by a second slower one due to the muscular contraction of the pharynx and œsophagus and which carries down any food that may have escaped the first movement and which forces it, together with the food that has already reached the cardiac orifice, through the latter into the stomach, the time elapsing from the beginning of deglutition amounting to about six seconds. If the region of the stomach be auscultated during deglutition at times two sounds may be heard, the first a "squirt sound" due to the projection of the bolus into the stomach by the contraction of the mylo-hyoid muscles, the second a "press sound" due to the action of the pharynx and œsophagus which occurs at the end of swallowing and which squeezes the residue of the food from the œsophagus into the stomach. It will be observed that under such circumstances the œsophagus contracts after the food just swallowed has passed into the stomach. While such appears to be the mechanism of the deglutition of water and of semi-fluid food, it should be mentioned that where a large mass of dry food or of considerable consistence is swallowed the mylo-hyoid muscles do not appear to contract with sufficient force to shoot the bolus down to the cardiac orifice, the muscular action of the pharynx and the œsophagus being necessary to accomplish this effect. In that case there is but one movement of deglutition and one auscultation sound, the "press sound," and the œsophagus contracts before the bolus passes into the stomach as in rabbits, for example, whose food is usually dry. The passage of the food through the pharynx and œsophagus are effected by means of muscular fibers which are disposed in the pharynx as the constrictors and in the œsophagus in two layers, an external longitudinal and an internal circular, the fibers being striated in the upper third, unstriated in the lower third, and mixed in the middle third of the tube. This disposition is interesting as accounting perhaps for the œsophagus contracting in three segments, and for the lower third remaining contracted for a short time after the food has passed into the stomach, thereby

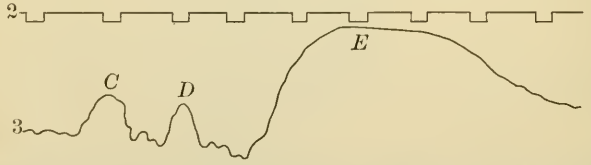
preventing regurgitation. The time elapsing during the contraction of each of the five muscular segments involved in deglutition and therefore of the total time between the beginning of deglutition and the moment that the bolus reaches the stomach is given in the following table :

TIME OF DEGLUTITION.

	Seconds.
Contraction of mylo-hyoids and constrictors of pharynx	0.3
Contraction of first part of œsophagus . . .	0.9
Contraction of second part of œsophagus . . .	1 8
Contraction of third part of œsophagus . . .	3.0
	6.0

It has also been shown that if a second act of swallowing is made within six seconds of the first one the pharyngeal œsophageal wave of contraction does not reach the stomach until six seconds after the second swallow, just as if this had been the only one, the second deglutition not only stimulating the œsophagus to contract, but inhibiting that part which, though stimulated, has not yet contracted. Such is also the case if we make several swallows successively, as in drinking a glass of water, the œsophagus not contracting until after the last swallow and after the same interval of time as would have elapsed if deglutition had only been performed once. The theory of deglutition that we have just described is essentially that first offered by Kronecker and Falk,[1] though afterwards much better established by Meltzer.[2] The method of experimentation made use of by the latter was to insert small rubber balloons in the pharynx œsophagus at different levels and to connect the same by tubes with a tambour and recording levers, the latter being placed together with the pen of a time-marker in contact with a kymograph. Such being the disposition of the apparatus, with an act of swallowing curves were produced upon the kymograph (Fig. 32), due to the

FIG. 32.



2. Line marking seconds. 3. Tracing of the bag in the œsophagus 12 centimeters from the teeth. *C.* Compression of the bag by the bolus. *D.* Compression by the residues of the bolus carried on by the contraction of the pharynx. *E.* Contraction of the œsophagus. (LANDOIS.)

pressure exerted upon the balloons by the bolus of food as it was first shot down by the action of the mylo-hyoid muscles, and, secondly, by the action of the pharynx and œsophagus. In accordance with the way the curves were produced, they always presented

[1] DuBois Reymond's Archiv, 1880, 1881, 1883.

[2] New York Medical Journal, 1894. Journal of Experimental Medicine, Vol. II., 1897, p. 453.

two elevations or one elevation with two crests, the first elevation or crest, due to the rapid, the second to the slow, contraction wave.

By such curves Dr. Meltzer determined in his own person, (1) the length of time elapsing between the beginning of deglutition and the moment that the food arrived at the stomach; (2) the interval of time between the two waves of contraction when the balloon was in the pharynx; (3) the time during which the food passed through the five contracting segments.

The act of deglutition is usually divided, for convenience of description, into three periods, stages, or movements:[1] (1) The passage of the bolus from the mouth through the fauces into the pharynx; (2) from the pharynx into the œsophagus; (3) from the œsophagus into the stomach. If the description of the process just given is regarded, however, as correct, the division into three movements, the limits of which in any case are entirely arbitrary, loses much of its significance and may as well be discarded. While the beginning of deglutition, or the part confined to the mouth, is voluntary, the remainder is involuntary in character, being due to an impression made upon the mucous membrane of the palate, etc., by the food, which stimulates the center in the medulla, from which emanate the impulses that pass to the muscles involved. Indeed, without solid or liquid food in the pharynx it is impossible to perform the second act of deglutition; apparently, this is done sometimes for three or four times without there being anything to swallow, but there is really always present, under such circumstances, sufficient saliva to produce the necessary impression.

It may be stated in this connection that the different parts of the œsophagus appear to contract independently of each other[2] the propagation of the contraction wave not depending upon the continuity of tissue since one or more segments of the œsophagus may be removed, and yet the remaining parts will contract in response to the stimulus of impulses passing from the medulla.

It is hardly necessary to call attention to the fact that solid and liquid foods can be swallowed in all positions. It is a common feat among jugglers to drink a bottle of wine or a glass of beer while standing on their heads or hands.

[1] Majendie, Thèse soutenue à l' École de Médecine de Paris, en 1808. Précis Elementaire de Physiologie, Tome ii., p. 59.

[2] A. Mosso, Moleschott, Untersuchungen, 1878, Band xi., s. 327. Kronecker ü. Meltzer; Du Bois Reymond, Archiv, 1881, s. 465.

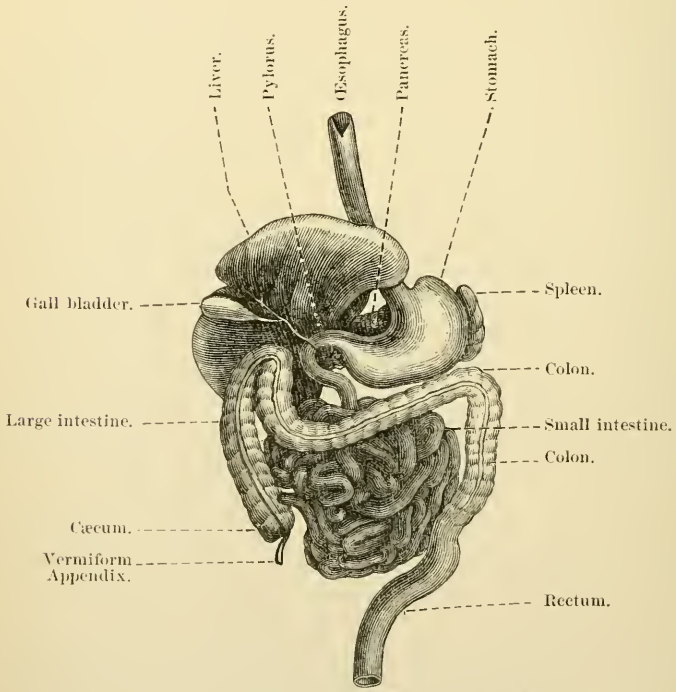
CHAPTER VII.

DIGESTION.— (*Continued.*)

GASTRIC DIGESTION.

The stomach is a musculo-membranous sac whose walls have on an average a thickness of a little more than two millimeters (a line). When distended it measures laterally about 37.5 centimeters (15 inches), and antero-posteriorly 12.5 centimeters (5 inches) with a capacity usually of 3 liters (5 pints). The capacity of

Fig. 33.



Digestive apparatus of man. (Milne Edwards.)

the stomach, however, is often less and sometimes even much greater, varying with the age, sex, and habit of the individual. It is held in position in the upper part of the abdominal cavity by its connection with the œsophagus and the folds of the peritoneum. When empty, the sides of the stomach are usually in contact, and the whole organ presents a flattened appearance. When distended by food, however, the anterior wall of the stomach becomes superior, and is applied to the diaphragm. This is due to the ends of the

stomach and lesser curvature being comparatively immovable. As the food enters the stomach from the œsophagus, it turns to the left, and, passing into the cardiac end, or greater pouch, thence proceeds along the greater curvature to the pyloric end, returning by the lesser curvature to the cardiac portion, to begin the same course over again. Each of these revolutions occupies from about one to three minutes, and are slowest at first, becoming more rapid as digestion advances. The food undergoes, therefore, a sort of churning action, passing from one side of the stomach to the other. Hereby it is thoroughly incorporated with the gastric juice, gradually broken down, liquefied, and finally converted into what is known as the chyme. During the beginning of digestion the pyloric orifice is so firmly closed by the contraction of the circular muscular fiber aided by the circular fold of mucous membrane developed there that no food passes into the duodenum. After the churning movement just described has continued, however, for about a quarter of an hour the circular muscular fibers of the pyloric orifice relax. Then the liquid pultaceous part of the food and later the more solid portions and even hard bodies, such as coins, stones, are pushed or forced into the duodenum by the vigorous peristaltic contractions of the pyloric part of the stomach, the fundus, or cardiac portion, taking little or no part, acting rather as a reservoir. Indeed, when digestion is at its height, the cardiac portion of the stomach is quite distinctly separated from the pyloric portion by a "transverse" constricting band, the so-called "sphincter antri pylorici" situated from seven to ten centimeters from the pylorus. The organ then presents an hour-glass form, of which two-fifths consist of the cardiac portion. It is worth mentioning in this connection, that this hour-glass form of the stomach, present only in man during digestion, is the form presented in the manatee whether digestion is going on or not; the author having found in the dissection of several individuals the stomach always presenting this form, whether it was full of food or empty.[1]

After the food has been digested and the stomach has been emptied of its contents, which processes are effected within a period of from two to four hours, all the motions just described cease, and do not recommence again until a fresh supply of food is taken. The churning and peristaltic motions of the stomach just described depend upon its muscular fibers assisted by the diaphragm. The muscular coat of the stomach which averages about a millimeter ($\frac{1}{25}$ of an inch) in thickness, consists of three sets of fibers, the longitudinal, circular, and oblique, which are disposed from without inward, in the order just named—that is, the longitudinal fibers are external, the oblique are internal, while the circular fibers lie between the other two.

These three sets of fibers are, however, very unequally developed. Thus, the longitudinal fibers are best seen in the lesser curvature;

[1] H. C. Chapman, Proc. Acad. of Nat. Sciences, Phila., 1876, p. 452.

the circular fibers are rather indistinct to the left of the cardiac orifice, and are most marked at the pyloric, forming then its sphincter muscle; while the oblique fibers are limited to the cardiac portion of the stomach, passing over it from left to right. It is at the point where these oblique fibers cease that the stomach becomes constricted in digestion into the two parts already described.

Through the contraction of the longitudinal and circular fibers the food is forced along toward the pylorus, which, through its sphincter muscle, resists at first as we have seen the passage of any food into the small intestines. The cardiac orifice is guarded by the fibers in that situation, as well as by the contraction of the lower part of the œsophagus already referred to. The movement of the food is also due, no doubt, partly to the pressure exerted by the diaphragm and the intestines. The natural stimulus to these motions of the stomach during digestion is the presence of food. The account that we have just given of the movements that the stomach undergoes during digestion in man, is based upon the experiments and observations made by Beaumont[1] upon St. Martin supplemented by those recently made upon animals.[2]

Alexis St. Martin, a voyageur in the service of the American Fur Company, a man about eighteen years of age, of good constitution, robust and healthy, was accidentally wounded by the discharge of a musket on the 6th of June, 1822. The charge, consisting of powder and duck shot, entered the left side posteriorly and obliquely, blowing off integument and muscles of the size of a man's hand, fracturing the sixth and seventh ribs, lacerating the lower portion of the left lobe of the lungs, the diaphragm, and perforating the stomach. Notwithstanding the serious nature of the wounds St. Martin recovered at least so far as concerned his general health. The perforation through the walls of the stomach, however, remained permanently open, having resisted all treatment. This perforation (Fig. 34) was situated three inches to the left of the cardiac portion of the stomach, near the superior termination of the great curvature, and measured about two and a half inches in circumference. The opening was closed under ordinary circumstances by a movable valve formed through a doubling of the coats of the stomach, which had been formed during the progress of the case, and which effectually prevented the escape of food. This valve could be easily depressed, when the interior of the stomach could then be examined.

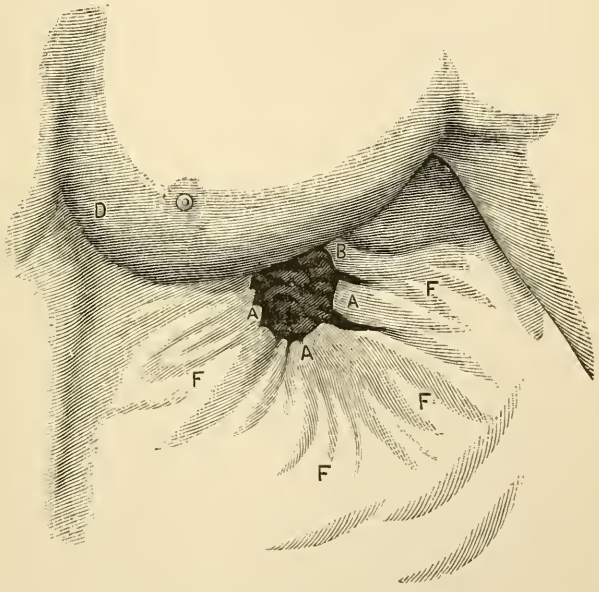
St. Martin, after the recovery of his health, performed all the duties of a common servant—chopping wood, carrying burthens, etc.—married and had several children and enjoyed general good health up to eighty years of age. For a number of years, off and

[1] Experiments and Observations on the Gastric Juice, Plattsburgh, 1833.

[2] Hofmeister and Schütz, Archiv für exper. Path. u. Phar., Band xx., 1886, s. 1. Rossbach, Deutsches Archiv für klinische Medecin, Band xlvi., 1890, s. 323. Moritz, Zeitschrift für Biologie, Band xxxii., 1895, s. 313.

on, St. Martin was under the observation of Beaumont, under strictly physiological conditions. It is this circumstance which makes this case so important in the history of the physiology of digestion, the cases of gastric fistula that had hitherto occurred [1] not having afforded much opportunity for the study of gastric digestion. It should be mentioned, however, that since the celebrated case of St. Martin interesting cases of gastric fistula, the result of wounds or gastrotomy, have been made use of for purposes of physiological investigation among others by Schmidt and Richet, the results of which will be referred to presently. Up to about the middle of the eighteenth century it was still a subject of discussion

FIG. 34.



Ordinary appearance of the left breast and side, the aperture filled with the valve; the subject in an erect position. (BEAUMONT.)

among physiologists as to whether the action of the stomach in digestion was of a chemical or purely mechanical nature. The controversy was finally, however, brought to a termination by the discovery of Reaumur,[2] in 1752, that there existed in birds a gastric juice, and that food was softened and partly digested in the stomach of those animals independently of any mechanical action of its walls. Reaumur's experiments consisted in inserting into the stomach of a bird (bustard) a tin tube containing meat, the ends of which were, however, covered with a grating, and permitting the tube to remain a sufficient time in the stomach for the gastric juice to mix with the food

[1] De Fistula Ventriculi, Robertus Marcus, Berolini, 1835.
[2] Memoires de l'Academie des Sciences, 1752, Tome lxix., p. 461.

and digest it, the walls of the tube resisting any pressure that might be exerted by the walls of the stomach. In substituting for the tube containing the meat small pieces of sponge, Reaumur was able to collect, by pressing the sponges after they had been rejected, a small quantity of a liquid which gave an acid reaction, and which was the first specimen of a solvent fluid from the stomach ever obtained. The next step in advance was made in 1777 by Edward Stevens,[1] who employed a juggler, whose habit was to swallow stones, to swallow instead little silver balls, which had previously been filled with different kinds of food, the walls of which, being perforated, permitted the entrance of the gastric juice. After twenty to forty hours these balls would be passed by the anus, and their contents would be found to be more or less digested. From the result of those experiments Stevens concluded that digestion cannot be accounted for by heat, trituration, putrefaction, or even fermentation alone, but by a most powerful humor which is secreted by the tunic of the stomach, and is poured into the cavity of the same.

A few years later there appeared the celebrated work of Spallanzani,[2] in which the observations of Reaumur and Stevens were repeated and confirmed, and extended in a series of experiments made upon quite a number and variety of animals including several interesting observations made by the author upon himself, some of which have already been alluded to in speaking of the subject of mastication. Spallanzani began his experiment upon himself by first swallowing little linen bags in which the different articles of food, animal or vegetable, were sewn up. These were usually passed by the anus within a period varying from twenty-three to twenty-four hours, and were found either empty or nearly so, the contents being more or less digested, according to the kind of food used and the length of time during which they had remained within the body. The necessity of first masticating the food before swallowing it was then demonstrated; and, in conclusion, a little gastric juice was obtained by vomiting, and the effect of this upon boiled beef tried outside the body, with the result of showing that the beef became pultaceous, and that there was no putrefaction. Spallanzani distinctly recognized a most important fact, that the process of digestion, beginning in the stomach, is completed in the intestines.

In 1803 a woman with a gastric fistula, coming under the care of Dr. Helm,[3] in Vienna, that physician profited by the opportunity to make some study of gastric digestion, but added little of value to what had already been established.

In 1824 Prout[4] endeavored to show, by analysis, that the acidity of the gastric juice in animals was due to hydrochloric acid.

Shortly afterward, between 1825 and 1827 simultaneously,

[1] De Alimentorum Concotione, Thesaurus Medicus Smellie, Tomus iii., p. 481.
[2] Fisica Animale e Vegetabile, Tomo secundo, Venezia, 1782.
[3] Jacob Helm, Zwei krankengeschiten, Vienne, 1803. Marcus, op. cit., p. 21.
[4] Philosophical Transactions, 1824.

Leuret and Lassaigne,[1] Tiedemann and Gmelin[2] made a detailed and extended series of observations upon digestion; those of the latter being the most elaborate. The experiments were made principally upon dogs, cats, horses, cows, sheep, birds, reptiles, and fishes, the observations on man being exceptional. In some of the experiments the means of obtaining the gastric juice were the same as those used by Reaumur, etc., already referred to. In many of them, however, another plan was adopted. The animal to be experimented upon after fasting, was made to swallow stones, nails, etc., a few hours afterward the animal was killed, it having been ascertained that such hard substances would excite the stomach to secrete a considerable amount of gastric juice—sufficient in quantity to analyze and experiment with. Notwithstanding the number of animals, experiments performed, and the variety of the observations, nothing definitely was established as to the composition and properties of the gastric juice, to what elements it owed its digestive powers, or exactly what effect it had upon different kinds of food. It will be seen, therefore, from this historical digression that little was positively known of gastric digestion, as it takes place in man, before the observations and experiments of Beaumont were made.

Beaumont was the first to observe digestion as it goes on in the healthy human stomach, to describe not only the motions of the latter, but also the manner in which the gastric juice is secreted, its effect upon food, the changes that food undergoes in the stomach, to collect the normal gastric juice in such quantities that it could be analyzed and studied with reference to its effect upon food outside the body, to determine the influence exerted, by temperature, exercise, and the nervous system, upon digestion, the length of time that food remains in the stomach, and numerous other interesting facts. Further, it was this remarkable case of St. Martin that first suggested to Bassow,[3] the Russian naturalist, the making of a permanent gastric fistula, afterwards also successively performed by Blondlot,[4] and frequently resorted to at the present day as a convenient means of obtaining fresh gastric juice.

Let us turn now to the consideration of the manner in which the gastric juice is produced, its composition, effect upon food, etc., as learned, by means of gastric fistulæ, from the examination of gastric juice obtained by the stomach pump, and from experiments made with artificial gastric juice.

During the intervals of digestion the stomach is empty, its mucous membrane being simply covered with a very thin, transparent, viscid mucus. At this time the reaction of the membrane is either faintly alkaline or neutral. With the introduction of food into the stomach, the membrane at once changes its pale appearance, becoming red and turgid from the increased amount of blood.

[1] Recherches pour Servir a l' Histoire de la Digestion. Paris, 1825.
[2] Recherches sur la Digestion. Paris, 1837.
[3] Bulletin de la Société des Naturalistes de Moscow, 1843, Tome xvi., p. 315.
[4] Traité analytique de la digestion, 1843.

Small drops of gastric juice appear as small pellucid points on the surface of the membrane, which has now an acid reaction, and gradually a little stream of gastric juice begins to flow upon the food in the stomach. Beaumont showed most conclusively that food is the natural stimulus to the secretion of the healthy gastric juice. For the exciting impression of food is diffused over the whole secreting surface, and the maximum effect is thereby obtained. Local stimulus, however, like that of an India-rubber tube, will excite a flow, and this Beaumont used when a small quantity of gastric juice—an ounce and a half, for example—was required unmixed with mucus or food.

The human gastric juice, which is rarely obtained free from food residues, mucus, and saliva, is a clear or faintly cloudy, almost colorless fluid, having a sour odor and taste, strong acid reaction and low specific gravity 1.001–1.010. As a general rule it contains also an admixture of glandular cells or their nuclei; mucous corpuscles and more or less changed cylindrical epithelium.

Composition of Gastric Juice.

The first to attempt to analyze the gastric juice was Scopoli, an Italian chemist, in the last century. The gastric juice examined was obtained by Spallanzani from a raven, and, according to Scopoli, consisted of an animal matter, earthy salts, and what would now be called hydrochloric acid. The gastric juice of St. Martin was examined among others by the late Professor Dunglison, who, in a letter to Beaumont,[1] states that it contained free muriatic and acetic acids, phosphates, and muriates, with bases of potassium, sodium, magnesium, and calcium, and an animal matter soluble in cold water, but insoluble in hot.

Among the more recent analyses of human gastric juice, that of the woman with a gastric fistula, made by Schmidt, is especially worth of mention.

Composition of Human Gastric Juice Holding Saliva.[2]

Water	994.400
Pepsin, etc.	3.195
Hydrochloric acid	0.200
Calcium chloride	0.061
Sodium chloride	1.464
Potassium chloride	0.550
Calcium, Magnesium, Ferrum phosphate	0.125
Loss	0.005
	1000.000

[1] Op. cit., pp. 78, 81.

[2] Annalen der Chemie, 1854, Band xcii., s. 46. Schmidt gives as the mean of the two analyses the numbers 994.404 for the water, and 1.465 for the sodium chloride. These are probably typographical errors, as the other numbers are those given in the table.

According to this analysis, then human gastric juice consists of water, pepsin, hydrochloric acid, chlorides, and phosphates. It should be mentioned, however, that the organic matter of the gastric juice consists not only of pepsin, but of another unformed ferment or enzyme, the so-called rennin. It would appear also from recent investigation that the amount of hydrochloric acid as given by Schmidt is too small, due probably to the gastric juice analyzed by him having been diluted with water or saliva. At least, Richet[1] found the hydrochloric acid of the human gastric juice also obtained from a fistula amounting as the average of eighty observations to 1.7 parts per thousand, the variation being from 0.5 to 3 parts per thousand, an estimate not differing essentially from the later ones of Szabo,[2] Ewald,[3] and Boas.[4] It may be mentioned that the samples of gastric juice analyzed by Szabo was taken from the stomach of a man by means of a stomach pump, without the addition of water.

The epithelium of the stomach consists of columnar cells, among which occur the so-called goblet, or mucus-secreting cells. The latter appear to be columnar cells, whose protoplasm has been transformed into mucinogen, or mucin, which swells up the cell at its free end, hence its name, as it passes into the cavity of the stomach. With the escape of the mucin, the more or less empty cell resumes the character of the ordinary columnar cell.

It has already been mentioned that the gastric juice is secreted by the mucous membrane of the stomach; let us consider now, so far as is known, the manner of its elaboration.

The mucous membrane of the stomach, in the living healthy subject, is of a velvety, pulpy consistence, with an average thickness of about 1.2 millimeters ($\frac{1}{20}$ of an inch), and in color of a pale pink or reddish appearance, which rapidly changes after death into a brownish hue. The mucous membrane is loosely attached to the submucous coat or the layer of areolar tissue which lies between the mucous coat within and the muscular coat without. It is through the looseness of this attachment that the longitudinal folds into which the membrane is usually thrown are due, and which are effaced when the stomach is distended. The epithelium presents, more particularly at the cardiac orifice, a marked contrast as compared with the pavement epithelium lining the œsophagus.

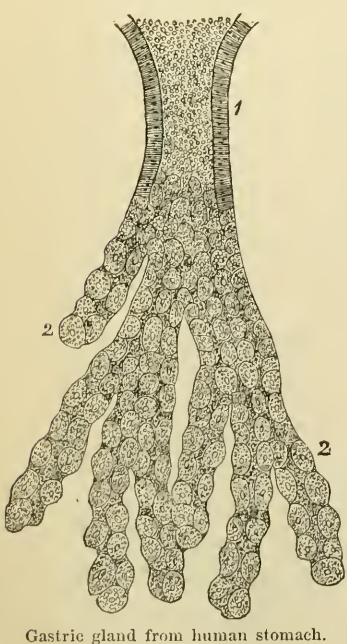
If the mucous membrane of the stomach be gently washed by allowing a small stream of water to run over it slowly, which will carry off the adhering mucus, and then be examined with a simple lens, little polygonal spaces or depressions will be noticed in its surface, varying in size from $\frac{1}{8}$ to $\frac{1}{4}$ of a millimeter ($\frac{1}{200}$ to $\frac{1}{100}$ of an inch) in diameter. If these depressions or alveoli be further exam-

[1] Comptes Rendus, Tome lxxxiv., p. 450, 1877.
[2] Zeitschrift für Physiologische Chemie, Band 1, 1877, s. 140.
[3] Die Lehre von Der Verdauung, 1879, s. 52.
[4] Deutsche Med. Wochenschr., 1892, Nr. 49, s. 1110. Diagnostik u. Therapie Der Magen Krankheiten, 1894, s. 20.

ined with the microscope, they will be seen to consist of a number of small round apertures of about $\frac{1}{200}$ to $\frac{1}{120}$ of a millimeter ($\frac{1}{5000}$ to $\frac{1}{3000}$ of an inch) in diameter. These minute apertures are the mouth-like openings of the gastric follicles, small tubules varying in length from 2 to 5 millimeters ($\frac{1}{12}$ to $\frac{1}{5}$ of an inch), and which are imbedded in the mucous membrane, the blind or closed ends of the tubules looking outwardly toward the submucous coat, the open ends inwardly toward the interior of the stomach.

The gastric tubules differ considerably in their structure and form, according to the part of the stomach examined. Thus, in the pyloric portion of the stomach the tubules are lined, to a certain extent at least, with a continuation of the columnar epithelium covering the inner surface of the stomach; in the upper parts, however, of these tubules the lining cells become shorter and more cubical in character, and correspond apparently in their function with the central[1] cells found in the tubules found in the cardiac part of the stomach. The pyloric tubules, while terminating usually in a branched manner, terminate also simply. If the middle zone of the stomach be now examined, both simple and branched tubules (Fig. 35) will be found resembling those in the pyloric portion, but while the upper portion of the tubule is lined with columnar epithelium, the succeeding part or neck is filled rather than lined by large ovoidal or spheroidal granular cells, the so-called parietal[2] cells. Toward the bottom or fundus of the gland these parietal cells do not form a continuous layer, but are seen scattered here and there, and bulging out so as to give the tubule a varicose appearance, the remaining portion of the tubule, except the narrow passage-way in the middle, being occupied by finely granular polyhedral angular cells, the so-called central cells, similar, as just mentioned, to those found in the pyloric tubules.[3] In the cardiac portion of the stomach, more particularly around the cardiac orifice, the tubules are branched in

Fig. 35.



Gastric gland from human stomach.
1. Columnar cells. 2. Parietal cells.

[1] Principal, chief, adelomorphous (ἄδηλος, hidden) cells.

[2] Ovoid, border, oxyntic (ὀξύνειν, to acidulate), delomorphous cells.

[3] According to the recent observations of Langendorff and Laserstein (Pflüger's Archiv, 1894, Band lv., s. 578) the main tube of a gastric tubule, at least those presenting parietal cells, not only extends throughout the length of the tubule as usually described, but gives off lateral branches, which pass to the parietal cells, and there forms a network on which the cell lies.

character, the upper part of the tubule dividing into two or three branches, and there usually subdividing again. These cardiac tubules, like simple ones found in the middle zone of the stomach, contain both ovoid and central cells. It will be observed from this brief description that two kinds of glands are found in the human stomach, differing essentially in their structure: pyloric tubules, simple and branched, situated in the pyloric part of the stomach, containing columnar and central cells: cardiac tubules, simple and branched, situated in the middle and cardiac parts of the stomach, containing columnar and central cells also.

While undoubtedly such a distinction as that just described exists between the gastric glands in man, the exact line of demarcation between the two is not as distinct as in certain animals, the dog for example, the different kind of glands passing in man into each other through intermediate forms. Judging from what has been learned of the process of salivary secretion, analogy would lead us to suppose that the gastric juice is secreted in an essentially similar manner, and such would appear to be the case, as shown more particularly by the researches of Heidenhain.[1] Thus, if sections of the gastric glands of an animal be examined before the taking of food, the so-called central cells of the cardiac, as well as those of the pyloric glands, will be found pale, finely granular, and not staining readily with aniline or carmine. With the beginning of digestion, however, these cells become swollen, coarsely granular, turbid, and stain more readily with the above reagents; as digestion continues, the coarse, granular, and turbid condition and disposition to stain increase, while at the same time the cells become smaller and shrunken. The only conclusion to be drawn from the changes in these cells is that the readily stainable material, etc., developed during digestion constitutes the antecedent stages, the mother substances, or zymogens of pepsin and rennin, the so-called pepsinogen and renninogen. Inasmuch, however, as the parietal cells of the cardiac portion of the stomach do not exhibit during digestion the histological changes observed in the central cells of the cardiac and pyloric glands, only swelling up and projecting somewhat externally from the wall of the gland, and from the fact of parietal cells being present in the glands of the stomach of the frog coincidentally with the presence of acid, the pepsin-forming cells being confined almost entirely to the lower part of the œsophagus in that animal, it appears reasonable to attribute to the parietal cells the production of the hydrochloric acid of the gastric juice. If such be the case, however, it is somewhat difficult to understand why, after injecting ferrocyanide of potassium and ferric lactate into the blood of an animal, as in the experiment of Bernard,[2] the production of Prussian blue should be limited to the surface of the stomach, since if the ovoid cells of the glands actually produce the

[1] Hermann, Handbuch, Funfter Band, 1880, s. 141.
[2] Liquides de l'Organisme, Tome ii., p. 375. Paris, 1859.

acid the presence of which is necessary for the formation of the salt, the Prussian blue should be visible in the cells of the fundus or their vicinity, as well as upon the surface or mouth of the gland, unless the acid is expelled from the gland as rapidly as produced, which is not improbable. If the above view be accepted as correct then the gastric juice is secreted by only the cardiac tubules, those containing parietal cells producing acid and central cells elaborating the zymogens, the cells of the pyloric tubules elaborating only the latter, and the columnar epithelial cells, mucus.[1] As a confirmation of this view it may be mentioned that an infusion of the mucous membrane of the pyloric portion of the stomach does not possess digestive properties unless acidulated. It will be recalled also in this connection, that in speaking of the motions of the stomach, attention was called to the fact of the cardiac portion of the stomach acting as a reservoir for the food, the pyloric portion as the expulsive part. The significance of this distinction becomes more apparent now that it has been shown that digestion is limited to the cardiac part of the stomach. The nature and chemical constitution of pepsin, although it was discovered many years since,[2] is still imperfectly understood, it not having been obtained as yet in a sufficiently pure state to admit of analysis. It is regarded as being an unformed ferment, an enzyme on account of its characteristic effect upon proteid matter. Like other ferments a small amount of pepsin will convert a large amount of proteid into peptone, the action of the pepsin being retarded like ptyalin by any great excess of the products of digestion. One of the most striking peculiarities of pepsin is that it only acts on acid media and upon albuminous bodies, the latter swelling up, becoming transparent, and then dissolving under its influence. Hence the gastric juice to be efficacious contains, as we have seen, both pepsin and hydrochloric acid. It should be mentioned that while hydrochloric acid can be replaced by certain acids such as lactic, nitric, or phosphoric acids, the latter are not so effective.

Like other enzymes the action of pepsin is influenced by temperature, the most favorable being about 38°C. (100°F.), while a prolonged exposure to one of 80°C. (176°F.) will destroy the enzyme. A solution of pepsin may be obtained relatively pure by treating the mucous membrane of the stomach with dilute phosphoric acid and then adding lime water. The resulting precipitate which carries down the pepsin being then dissolved with dilute hydrochloric acid and the salts removed by dialysis, the non-diffusible pepsin remains in the dialyzer. Rennin, derived from zymogen rennin by the action of an acid and whose chemical construction is still unknown, is regarded as being an enzyme on account of the

[1] According to more recent investigations the changes undergone by the cells during digestion are somewhat different from those described in the text. The results, however, can be reconciled to a great extent if the different conditions under which the cells were examined be taken into consideration. J. N. Langley, Journal of Physiology, 1880, Vol. II., p. 261.

[2] Schwann, Müller's Archiv, 1836, s. 66.

property it possesses of coagulating or curdling milk. Some difference of opinion still prevails as to the nature of the process of curdling. Recent researches render it probable, however, that the casein of milk[1] is split by rennin into two bodies, one of which, paracasein (cheese), in combining with calcium salts is precipitated as the insoluble curd, while the other, the "whey proteid," remains in solution. There appears to be no doubt that the curdling of milk does not take place in the absence of calcium salts. There is still some difference of opinion, however, whether the latter act by combining with the paracasein to form an insoluble compound, the curd, or whether they influence, in some way, the separating out of the paracasein. Although the chemical nature of rennin is as little understood as that of pepsin, that it is an enzyme is still further shown by the fact that one part will precipitate 800,000 parts of casein.[2] It might be supposed that the curdling of milk in the stomach was due to the acid of the gastric juice, since casein is precipitated by lactic acid, developed from lactose by bacteria, as in the souring of milk. Apart, however, from the fact of the casein not being split into curd and whey by the acid but is simply precipitatic as such, curdling will take place even after the gastric juice has been rendered neutral, but will not take place if the latter is boiled, the elevated temperature destroying the enzyme. The advantage of the curdling of milk in the stomach is not apparent, unless it be supposed that its digestion is promoted when in that condition. That such is the case is rendered probable, however, from the fact that the curd is readily digested by the gastric juice, being converted into peptone like other proteids. A comparatively pure solution of rennin may be obtained according to Hammarsten[3] in the following way: An infusion of the mucous membrane of the stomach being acidulated with hydrochloric acid, is just neutralized and then shaken with magnesium carbonate until the pepsin is precipitated. The filtrate being precipitated with basic lead acetate is decomposed with very dilute sulphuric acid, and the acid liquid filtered and treated with a solution of stearin soap. The rennin is precipitated by the fatty acids set free, and when the last are placed in water, and removed by shaking with ether, the rennin remains in the watery solution.

Hydrochloric Acid of the Gastric Juice.

The hydrochloric acid produced by the parietal cells of the cardiac tubules appears to be derived from the decomposition of the

[1] Casein is sometimes called caseinogen, in which case paracasein is named casein. The term caseinogen, if we wish to be consistent in our nomenclature, should be reserved, however, for a mother substance of casein which may yet be shown to exist in the cells of the mammary glands, as pepsinogen, the mother substance of pepsin, exists in the gastric glands.

[2] Landois, A Text-book of Human Physiology. Translated by Stirling, 1891, p. 306.

[3] Hammarsten, op. cit., p. 184. J. W. Warren, M.D., On the Presence of a Milk-curdling Ferment (Pexin) in the Gastric Mucous Membrane of Vertebrates, Journ. of Exp. Med., Vol. 2, 1897, p. 475.

sodium chlorides of the blood supplied by the food through the action of the primary acid sodium phosphate,[1] the reaction being as follows:

$$NaCl + NaH_2PO_4 = HCl + Na_2HPO_4$$

In confirmation of the above view, it may be mentioned that during gastric digestion in the dog, while the excretion of chlorides diminishes, the alkalinity of the urine increases, the sodium carbonate ($NaHCO_3$) to which the latter is due, being the final form assumed by the sodium liberated in the decomposition of the chlorides.[2] On the supposition that the secondary sodium phosphate (Na_2HPO_4) formed according to the above reaction remains in the blood and meets there carbon dioxide and water it becomes intelligible how through mutual reaction, the sodium carbonate of the urine may be formed. Thus

$$Na_2HPO_4 + CO_2 + H_2O = NaH_2PO_4 + NaHCO_3$$

As a further proof that the hydrochloric acid of the gastric juice is derived in the manner just mentioned, it may be stated that, according to recent experiments,[3] if a dog be given with his food sodium bromide instead of sodium chloride, more than fifty per cent. of the hydrochloric acid of the gastric juice will be replaced by hydrobromic acid. In this connection it should be stated, however, that when sodium iodine is given instead of sodium chloride the gastric juice contains but little hydroiodic acid. The greater part of the hydrochloric acid present in the gastric juice is regarded as existing in a free state. From the fact, however, that pepsin will convert proteid into acid albumin like hydrochloric acid, though more slowly, as well as for other reasons, it is inferred that part of the hydrochloric acid at least exists in combination with pepsin as a "paired acid," pepsin-hydrochloric acid. The existence of an acid in the free state as in the case of the hydrochloric acid of the gastric juice, though a rare occurrence in the animal economy, is not the only one known. Many years since it was observed by Troschel[4] on a visit to Messina that the salivary glands of the Dolium galia, a gastropodous mollusk, excreted a fluid containing free mineral acids shown afterwards by Boldeker to be hydrochloric and sulphuric acids.

Action of Gastric Juice Upon Food.

Let us turn now to the consideration of the action of the gastric juice upon the different articles of food as learned either from experiments made with the normal secretion obtained from gastric fistulæ, with artificial gastric juice, and from an examination of the contents of the stomach. It may be mentioned in this connection that an

[1] Maly, Hermann, Handbuch, 1881, Band v., Zweiter Theil, s. 67.
[2] E. O. Schoumow-Sumanowski, Archiv für exper. Path. u. Phar., 1894, Band 33, s. 336.
[3] Neucki u. Schoumow, Idem, Band 34, 1894, s. 313.
[4] Poggendorff's Annalen, Band 93, s. 614, 1854.

artificial gastric juice can be readily prepared by adding a glycerine extract of the mucous membrane of the stomach to a large bulk of 0.3 per cent. hydrochloric acid. When the gastric juice so prepared is used for showing the digestion of proteids and certain albuminoids, to which we shall see its action is limited, the temperature should be maintained at about 37°C. (100°F.), and the mixture stirred from time to time. When meat is subjected to the action of gastric juice, whether obtained from a fistula in the stomach or artificially prepared, it gradually becomes softer, changes in color, and breaks down into a grumous, pultaceous mass. Under the microscope the muscular fibers, though broken up into small pieces and retaining but little tenacity, are readily recognized through their characteristic striæ. The intermuscular connective tissue, the sarcolemma, disappears, however, being completely dissolved out. Meat is, therefore, not actually dissolved in the stomach, but is rather disintegrated and converted into a pultaceous liquid, which readily passes into the small intestine.

In a similiar manner white of egg, fibrin, the casein of milk, gelatin, glutin, etc., are broken down, liquefied, and converted into a grayish soup-like liquid. The gastric juice, however, not only acts physically upon the albuminous, proteid foods, softening, disintegrating, and liquefying them, but chemically also, transforming them into peptones,[1] albumin, becoming albumin peptone, gelatin, gelatin peptone, etc. The transformation of proteid into peptone by the action of the gastric juice according to the generally accepted [2] view is essentially as follows: The proteid is first converted by the hydrochloric acid into acid albumin or syntonin, the latter then, under the influence of the pepsin, takes up water, and splits into two substances, viz., hemialbumose and antialbumose which passing through intermediate stages finally become hemipeptone and antipeptone, a mixture of the two latter being called amphopeptone. Peptones have hitherto been separated from their antecedents, the so-called albumoses or proteoses[3] by saturating a mixture containing them both, with ammonium sulphide, it being supposed that all of the proteids present would be precipitated except the peptones. As there is good reason however for supposing that certain of these intermediate products of proteolytic digestion (deuteroalbumose) are not precipitated, some doubt[4] still exists as to whether peptones have ever been obtained pure. Further, the only way by which the hemipeptone can be separated from the antipeptone in the amphopeptone mixture or the final product of peptic digestion depends

[1] Lehmann, Lehrbuch der Physiologische Chemie, 1853, Band ii., s. 46.

[2] Kühne, Verhand Nat. Hist. Med. Vereins, N. F., Band i., Heidelberg, 1876. Neumeister, Lehrbuch der physiologischen Chemie, 1897, s. 231. Chittenden, Cartwright Lectures, Medical Record, New York, 1894, pp. 485, 516, 545.

[3] The term proteose is sometimes used as synonymous with albumose, sometimes in a more general sense as including albumoses. From the latter point of view albumose derived from albumin, caseose from casein, etc., would be regarded as proteoses.

[4] Hammarsten, op. cit., p. 28.

upon the fact, as we shall see hereafter, that while antipeptone resists all further digestion, hemipeptone is decomposed through the action of the trypsin of the pancreatic juice into the amido acids leucin and tyrosin. It is obvious however that while this method suffices for the obtaining of antipeptone it necessarily involves the destruction of the hemipeptone.

Indeed the existence of the latter peptone is rather an inference from the fact that through the action of trypsin upon amphopeptone two bodies appear, leucin and tyrosin, of which hemipeptone is supposed to be the antecedent.[1] A convenient method of showing the conversion of proteid into peptone by gastric juice and at the same time the necessity of the latter containing both pepsin and dilute hydrochloric acid is as follows: Prepare three cubes of equal size of coagulated white of egg, put one cube into a test-tube containing gastric juice, another into a second tube in which the gastric juice has been boiled that is in a weak solution of hydrochloric acid (0.2 per cent), the pepsin having been destroyed, a third in a tube in which the gastric juice has been neutralized that is in a solution of pepsin (0.3 per cent.). After a few hours if the temperature be maintained at about that of the body and the mixture stirred from time to time it will be found that, while the albumin in the gastric juice has been reduced to a grumous condition converted into amphopeptone, that in the boiled gastric juice or the weak solution of hydrochloric acid has only been transformed into syntonin, and that in the neutralized solution or the solution of pepsin but little if at all modified, some syntonin being formed if the action be prolonged. Peptones from whatever proteids they may be derived, whether albumin, fibrin, casein, etc., and, however derived, while differing somewhat from each other in their ultimate composition, are generally characterized by the following properties: They are completely soluble in water and diffuse readily through animal membranes, the latter property rendering them susceptible of absorption which the proteids from which they are derived are not. They are precipitated from neutral or feebly acid solutions by mercuric chloride, tannic acid, bile acids, and phospho-molybdic acid, but are not precipitated by boiling, by nitric or acetic acids, or potassium ferrocyanide. They give a red color with Millon's reagent (mercuric nitrate in nitric acid), a yellow color with nitric acid, the xanthoproteic reaction; a rosy red color with Fehling solution, the biuret reaction. They rotate the plane of polarized light to the left. It has already been mentioned incidentally that the gastric juice acts only upon proteids and albuminoids. Thus, for example,

[1] It must be admitted that considerable difference of opinion still prevails as to exactly the manner in which proteid is converted into peptone. Indeed, according to a recent authority, we know nothing certain at the present time concerning the essence of peptonization. We know not whether peptones are splitting products of albumin—still less whether the splitting products so arising resemble or differ from each other—or whether the peptones arise through a change in the position of the atoms without modification of the size of the molecule or through a taking up of water. Bunge, op. cit., s. 180.

while the gastric juice dissolves the albuminous wall of the fat vesicle, thus setting the fat free, it has no effect upon the fat itself. Gastric juice does not act upon carbohydrates. Any starch, for example, that may be converted into maltose or dextrose in the stomach is due to the saliva swallowed or possibly to gastric mucus.

It was shown many years since[1] and also more recently[2] that cane sugar is converted in the stomach into glucose. This effect appears to be due, however, not so much to the gastric juice proper as to its hydrochloric acid, since a 0.2 per cent. solution of the latter converts cane sugar into glucose and levulose outside of the body. It is possible also that the cane sugar converted into dextrose in the stomach may be due to a soluble enzyme. As the conversion of cane sugar into glucose takes place very slowly in the stomach it is not usually thought that any great amount of glucose is produced in this part of the alimentary canal. The action of the gastric juice in this respect may be, however, more important, at least in man, than is generally supposed, since, as we shall see hereafter, there is still some doubt as to exactly how cane sugar is converted into glucose in the small intestine. Submaxillary mucin and elastin are dissolved by the gastric juice, the latter but slowly, however. Neither keratin, or nuclein are dissolved by the gastric juice, hence the cell nucleus is insoluble in the latter. While the membrane of the vegetable cell is not dissolved by the gastric juice, that of the animal cell is, but less readily, in proportion as it approximates in composition to keratin. Oxyhæmoglobin, or the coloring matter of the blood, is decomposed by the gastric juice into hæmatin and acid albuminate. Hence the blood is changed in the stomach into a dark brown mass. According to the observations of Beaumont, bones were dissolved, to a certain extent at least, by the gastric juice, while water, alcohol, and other fluids[3] appeared to be absorbed in the stomach as such or to pass unaffected into the intestine.

It is well known under certain circumstances that the coats of the stomach itself are unaffected by the action of the gastric juice during life, but are digested after death. It is said that when one of the old alchemists announced that he possessed a universal solvent, the question was at once asked in what did he keep it. Naturally enough it was asked in the last century of those who held that the gastric juice would dissolve organic substances, why it did not act upon the stomach itself. We have seen, however, that the gastric juice does not digest all kinds of organic food, but that its action is limited rather to particular kinds of it, it having no action upon fat, starch, epidermis, etc. The answer would then appear to be, that the stomach is lined with some substance that the gastric juice does not act upon. According to this idea Ber-

[1] Bouchardat et Sandras, Supplément à l'Annuaire de thérapeutique, pour 1846, p. 83.

[2] Leube, Virchow's Archiv, 1882, Band 88, s. 222.

[3] Op. cit., p. 97.

nard[1] held that the lining epithelium of the stomach protected it from the gastric juice, assuming that the epithelium was as constantly renewed as destroyed. A confirmation of the view that the epithelium lining of the stomach gives it its immunity from digestion during life, is shown by the fact that worms, like the thread-worm, ascaris, etc., whose body wall is covered with epithelium, are able to live in the stomach, bathed at times in gastric juice. After the death of the worm, however, from any cause, the mouth or anus being opened, then the gastric juice is able to penetrate within its body and will then act upon the viscera until often nothing will be left of the worm except its outer body wall, which will float about in the stomach, unaffected by the gastric juice. In the same way, if the epithelium of the stomach be loosened from the parts beneath, it will be found undigested in the gastric juice; as a matter of fact, it is not digested whether living or dead any more than the skin of the ascaris is digested. There is no reason for assuming, then, that during life it is rapidly regenerated because it is constantly being destroyed. After death the epithelium loosening itself from the coats of the stomach, the latter will no doubt be attacked by the gastric juice, the epithelium itself remaining unaffected. It must be admitted that this explanation is not entirely satisfactory, being open to objections like all other explanations that have been offered. It presents, however, this advantage, that it does not invoke the aid of a vital spirit,[2] nor of catalysis,[3] nor does it attribute to the alkalinity of the blood a preserving power in the stomach that it does not possess in the intestine,[4] but depends simply upon the fact as to whether or not epithelium alive or dead is digested by the gastric juice.

One of the most interesting facts connected with gastric digestion is the entire absence of putrefaction. It was long since observed[5] that meat does not putrefy, at least for a long time if kept in gastric juice, while the normal secretion itself remains perfectly free from putrefaction even months after withdrawal from the stomach. This effect of the gastric juice is undoubtedly due to its hydrochloric acid, which exerts an anti-fermentative action. If, however, the gastric juice is neutralized, then a fermentation is set up in the stomach whereby lactic and other organic acids are generated. The hydrochloric acid, like weak mineral acids, acts also as an antiseptic, at least to some extent. Thus the cholera bacillus, varieties of streptococcus infecting wounds, the staphylococcus pyogenes aureus are killed by the gastric juice. Since the hydrochloric acid prevents fermentation with the generation of gases, the nitrogen (72.5 per cent.), carbon dioxide (20.7 per cent.), and hydrogen (6.7 per cent.) that are found (Planer) in the stomach[6] are either derived from

[1] Physiologie Experimentale, 1856, Tome II., p. 404.
[2] Hunter, Phil. Transactions, London, 1772, p. 447.
[3] Dalton, Physiology, 2d edit., 1861, p. 132.
[4] Pavy, Phil. Transactions, London, 1863, p. 169.
[5] Spallanzani, op. cit., pp. 107–308. [6] Landois, op. cit., p. 308.

the air and saliva swallowed, or, being generated in the intestine, pass backward into the stomach. As the oxygen that passes into the stomach is absorbed by the blood little or none is found there, it being replaced by carbon dioxide in the proportion of one volume of the former to two of the latter.

It is impossible to state exactly the amount of gastric juice secreted by a man during the twenty-four hours. Approximately it may be said to amount to about seven kilogrammes (15.4 pounds) daily. This estimate is based upon the amount of gastric juice absolutely collected from animals whose weight was compared with that of an adult man, and by the amount of gastric juice necessary to digest a known quantity of meat, one gramme of meat requiring 13.5 grammes of gastric juice. It must be remembered, however, that the amount of gastric juice secreted varies with the kind of food, and even with the same food under different circumstances. Further, as the gastric juice is reabsorbed with the food, there is some risk of counting the same gastric juice, or at least the elements of the same over again. Moreover, it has been shown that the amount of gastric juice secreted will vary considerably according to the chemical nature of the contents of the stomach. Thus, while water and peptones, particularly the latter, promote in a marked degree the secretion of the gastric juice, acids, alkalies, and neutral salts have in this respect but little effect.[1]

DIGESTION OF FOOD IN STOMACH.[2]

Kind of food.	Time.
Pig's feet, tripe	1 hour.
Salmon, trout	1 "
Barley soup	1 hour 30 min.
Milk	2 hours.
Potatoes, roasted; beans, boiled	2 "
Roast turkey	2 hours 30 min.
Soft boiled eggs	2 " 30 "
Beefsteak, broiled	2 " 30 "
Pork, raw	3 hours.
Hard boiled eggs	3 "
Mutton soup	3 hours 30 min.
Oyster soup	3 " 30 "
Potatoes, boiled	3 " 30 "
Beef and vegetable soup	3 " 30 "
Duck, roasted	4 hours.
Veal, broiled	4 "
Veal, fried	4 "
Pork, boiled	4 hours 30 min.
Cabbage, boiled	
Pork, roasted	5 hours 15 min.

It will be observed from the observations of Beaumont, that certain articles of food are digested in the stomach much more rapidly

[1] Khigine, Archives des Sciences Biologique, St. Petersburg, 1895, Tome III., p. 461.

[2] Beaumont, op. cit., p. 269.

than others. Thus, pig's feet, tripe, are digested in one hour, milk and roast potatoes in two, soft boiled eggs in three hours, hard boiled in three and a half, roast duck in four, while roast pork requires for its digestion more than five hours. It is highly probable, however, that when the food is liquid in character, water, for example, it remains in the stomach but a short time, not longer, perhaps, judging from experiments upon dogs, than from twenty to thirty minutes. It must not be supposed, however, that because certain articles of food are slowly digested, that necessarily they will give rise to uneasiness or inconvenience in the stomach, but there are times when the administration of food, with reference to its rapid digestion, becomes of vital importance. Thus, in certain critical periods of disease, when a life hangs upon a thread, when every moment that life can be prolonged is invaluable, the judicious administration of food that can be easily and quickly digested and absorbed may be the only means of saving the patient. It must be borne in mind that the natural stimulus of the gastric juice is the presence of food, and that for the time being there is a limit to the amount of this secretion, like all others. Hence, whenever there have been great prostration of strength and loss of tone, the stomach, enfeebled like the rest of the body, can digest but little; food under such circumstances should be given cautiously, both in quantity and quality.

From a great number of experiments performed upon St. Martin, Beaumont[1] concluded that the natural temperature of the human stomach was 100° F. (37.7°C.), and that the injection of food into the stomach did not elevate the temperature. The importance of heat in digestion will be seen when this function is contrasted in the hot- and cold-blooded animals; in the latter, where the heat of the body is about that of the surrounding air during winter digestion stops altogether, or goes on very slowly; while in the former, the temperature being independent of external conditions, at least within narrow limits, digestion goes on independent of change in the season.

In reference to the influence of exercise upon digestion, Beaumont observed that moderate exercise conduces considerably to healthy and rapid digestion; severe and fatiguing exercise, on the contrary, retards it. This is readily understood when it is remembered that exercise elevates the temperature and accelerates the circulation. On the other hand, if too much blood is diverted from the stomach to the brain or extremities by much mental or physical exercise indigestion ensues. No rules, however, can be laid down absolutely in this respect. In some individuals there is an uncontrollable desire to sleep after eating, the good effects of which are so evident that it is absurd to resist the feeling, whereas, in other cases, gentle exercise is equally imperatively demanded.

It is a matter of common observation that animals, as a general

[1] Op. cit., pp. 273, 276.

rule, take little or no exercise after eating. That digestion is retarded, and even entirely stopped, by too much exercise, the author has had ample opportunities of observing from post-mortem examination made both on human beings and animals who had eaten food a short time before death, and who were known to have taken a considerable amount of, and often violent, exercise during that period. Other physiologists seem to have had the same experience. Thus, in the last century, as related by Saunders,[1] Dr. Harwood, of Cambridge, procured two dogs, equally well fed; one of these he kept quiet, the other he compelled to take constant exercise immediately after eating. A few hours after feeding, both dogs were killed. The food was found entirely digested in the stomach of the dog that had been kept quiet, while in that of the one that had been compelled to take the exercise, the food was undigested.

Every one knows from experience, how digestion is influenced by the nervous system—a bad piece of news, a sudden shock, stopping digestion entirely, perhaps for hours. Beaumont observed that whenever the nervous system was disturbed or depressed by anger or fear, by undue excitement, from stimulating liquors, from overloading the stomach, etc., the mucous membrane became pale and moist or red and dry, and the secretions vitiated, diminished, or altogether suppressed.

It will be observed from what has been said of the action of the gastric juice upon food that gastric digestion must be of a preparatory character fitting the food for further digestion. Not only the carbohydrates and fats pass through the stomach practically unchanged, but even a part of the proteid, the hemipeptone moiety does not undergo complete digestion until it reaches the small intestine. It is for this reason that it is possible to remove the stomach almost entirely from an animal, a dog, for example, without apparently its health being materially affected;[2] at least a dog has lived for years after its stomach was removed and in good health.[3] It should not be inferred, however, from such an experiment that the stomach is a useless organ, but rather one which in converting the food into chyme, so modifies it as to make it more fit for further digestion in the small intestine.

[1] A Treatise on Structure, Economy, and Diseases of the Liver, London, 1803, p. 201.

[2] F. F. Kaiser, Beiträge zur Operativen Chirurgie, Czerny, 1878, s. 141.

[3] M. Ogata, Du Bois Reymond's Archiv, 1883, s. 89.

CHAPTER VIII.

DIGESTION.— (*Continued.*)

INTESTINAL DIGESTION. INTESTINAL JUICE. PANCREATIC JUICE. LIVER. GLYCOGEN. BILE. FECES. DEFECATION.

We have seen that shortly after food is taken into the stomach it passes in small quantities through the pyloric orifice into the small intestine, or the part of the alimentary canal intervening between the stomach and the ilio-cæcal valve. The small intestine is a cylindrical tube and in situ measures on an average from 5 to 6 meters (15 to 18 feet), but when separated from the mesentery or the peritoneum, which holds it in position in the abdominal cavity, it will be found to be a little longer—6.2 meters (about 20 feet). It has a diameter of about 3 centimeters (1.2 inches).

The small intestine is composed, in addition to its external or peritoneal coat, of two others : of a mucous membrane, including an epithelial and submucous or fibrous coat, and of a muscular coat lying exteriorly between the peritoneum and the mucous membrane. The muscular coat consists of unstriped muscular fiber, arranged in two layers, longitudinally or parallel with the long axis of the intestine, and circularly or at right angles with the axis ; the circular fibers being better developed than the longitudinal ones.

Peristaltic Movement of Intestine.

It is the slow and gradual contraction and relaxation of these muscular fibers that gives rise to the so-called peristaltic or vermicular movement by which the food is propelled along the intestine. The peristaltic motion of the intestine is well seen in an animal when opened in pure digestion. What is positively known, however, of the intestinal movements in man is derived from pathological cases where the abdominal walls were so thin that the motion could, to a certain extent, be seen and felt, or from cases of intestinal fistulæ to be presently referred to again.

Like the movements of the stomach, the natural stimulus to the vermicular motion of the intestine is the presence of food, during the intervals of digestion the intestine being at rest.

The peristaltic movement, as learned either from observations upon animals or man, is usually propagated from the stomach towards the cæcum, the wave during digestion passing over a distance of one centimeter ($\frac{2}{5}$ inch) within a period of from 20 to 50 seconds.[1]

The movement is easily retarded or even brought to a standstill

[1] Cash, Proc. of the Royal Society, London, 1887, vol. 41, p. 212. Fubini, Landois, op. cit., p. 283.

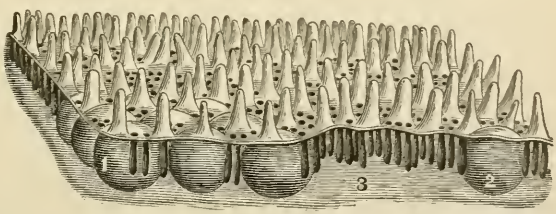
by a slight resistance, the contractions of the muscular fibers not being powerful. It is an interesting fact that if a small piece of intestine is resected and then placed within the abdominal cavity, but with its natural lower end sutured to the upper portion of the intestine food will pass from below upwards, accumulating in the upper portion of the intestine and causing dilatation.[1] Experiments of this kind appear to indicate that the propagation of the peristaltic motion in the normal direction depends upon some peculiar disposition of the muscular fibers. Nevertheless under certain circumstances anti-peristalsis may occur, that is, the normal movement is reversed, passing from the cæcum to the stomach.[2]

In addition to the peristaltic movement of the small intestine, the loops of the latter often exhibit a rhythmical to and fro movement, the so-called pendular movement. As at such times the blood is expelled from the submucous venous flexus by the contraction of the circular muscular fibers it is possible as suggested by Mall [3] that this movement promotes the circulation of the blood in the intestine, and aids in maintaining the pressure of the blood in the portal vein.

Valvulæ Conniventes and Villi.

Before turning to the consideration of the intestinal secretions, attention should be called to a peculiar disposition of the mucous membrane of the intestine, which, to a certain extent, retards the passage of the food and exposes it longer to the digestive fluids and to a greater absorbing surface. We refer to the villi and the valvulæ conniventes. On opening the small intestine and gently washing it, one will observe that instead of it being smooth, it presents a velvety appearance. This is due to the mucous membrane (Fig. 36) being raised up into millions of little cones or

Fig. 36.



Portions of the mucous membrane from the ileum, moderately magnified, exhibiting the villi on its free surface, and between them the orifices of the tubular glands. 1. Portion of an agminated gland. 2. A solitary gland. 3. Fibrous tissue. (Leidy.)

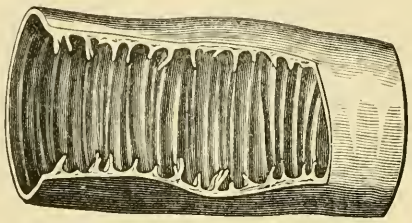
cylinders, the villi, which project inwardly into the cavity of the intestine. As these little structures are intimately connected with the subject of absorption, our account of their anatomy will be de-

[1] Mall, Johns Hopkins Hospital Reports, Vol. 1, 1896, p. 93.
[2] Grützner, Deutsche Med. Wochenschrift, 1894, s. 897.
[3] Op. cit., p. 37.

ferred until the next chapter, merely mentioning them here as offering a certain amount of resistance to the passage of food, just as any roughened surface offers resistance as compared with a smooth one to a substance passing over it.

While the villi are found all through the small intestine, the valvulæ conniventes, which have the same function in this respect, are restricted to a certain portion of it, being absent in the upper half of the duodenum and in the lower third of the ileum. The valvulæ conniventes (Fig. 37) are duplicatures of the mucous membrane extending transversely across the intestine at right angles to

FIG. 37.



Portion of small intestine laid open to show valvulæ conniventes. (BRINTON.)

its long axis, and occupying usually one-third or a half of the circumference, and sometimes extending all around the tube. The folds are widest in the middle, measuring often 12½ millimeters (about ½ inch). On either side of the middle line they thin away until they are lost in that part of the mucous membrane attached to the muscular coat. Inasmuch as there can be counted usually over 800 of these folds, it can be readily understood how the extent of the mucous membrane is increased by them. Naturally the food will take a longer time to pass over and between these barriers, so to speak, than over a plane surface, and this is of advantage in digestion and absorption, as the food will be more thoroughly incorporated with the secretions and have a better chance of being absorbed.

It is often stated that the valvulæ conniventes are only found in the intestine of man. This is incorrect, as they are present not only in the gorilla, chimpanzee, and orang,[1] but also in the ox, llama, camel, elephant, and ornithorynchus. They are remarkably well developed in the sharks, giving rise in those animals to the so-called spiral valve. Merely mentioning that the solitary glands and patches of Peyer, also found in the small intestine, will be described when the subject of the blood is considered, let us pass on now to the study of the intestinal and pancreatic juices and the bile and of the rôle that these secretions play in digestion.

As the food passes into the small intestine it becomes incorporated with the bile, the pancreatic and intestinal juices. The first two

[1] H. C. Chapman, Proc. Acad. Nat. Sciences, 1880, p. 166.

secretions pass into the duodenum from the liver and the pancreas respectively; the last, however, is secreted by glands found all through the intestinal tract. While the changes that the food undergoes in the small intestine are due to the simultaneous effects of these secretions, it is better, however, to study the effects of each separately whenever possible, in order to ascertain their relative importance in digestion? We will begin, then, with the intestinal juice.

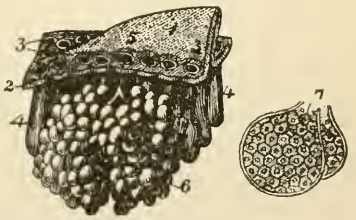
Intestinal Juice.

The intestinal juice, or succus entericus, consists, in the upper part of the intestine, of a mixture of the secretions of Brunner's and Lieberkühn's gland, but in the lower part, of the secretion of Lieberkühn glands alone. The glands of Brunner are confined to the duodenum, those of Lieberkühn occur throughout the small intestine.

Glands of Brunner.

The succus entericus, as it is also called, is secreted by two kinds of glands, the glands of Brunner or Brunn and the follicles of Lieberkühn. The former are confined to the duodenum; the latter, however, are found not only in the small intestine but in the large intestine also. The duodenal or glands of Brunner (Fig. 38) are branched tubular glands; they average about a millimeter ($\frac{1}{25}$ of an inch) in diameter and to the naked eye appear like little round bodies in the submucous tissue. The excretory duct, which transmits the secretion from the grape-like masses of which the gland consists, pierces the mucous membrane and opens into the cavity of the intestinal canal.

Fig. 38.



A vertical section of the duodenum highly magnified. 1. A fold-like villus. 2. Epithelium of the mucous membrane. 3. Orifices of the tubular glands, 4. 5. Orifice of a duodenal gland, 6. 7. Two vesicles of the latter, more highly magnified, exhibiting the epithelial cells lining their internal surface. (Leidy.)

According to Hirst and Heidenhain,[1] the cells of Brunner's glands exhibit essentially the same changes during periods of rest and activity as those of the pyloric tubules of the stomach, being large and clear during the period intervening between meals and small and cloudy during digestion, the secretion being elaborated during the former period and poured out during the latter.

The reaction of the secretion is alkaline. According to Grutzner,[2] it will digest fibrin in an acid solution, and Budge[3] and Krolow state that a watery extract will convert starch into sugar. Beyond these facts nothing is known positively of the properties of the secretion of Brunner's glands.

[1] Hermann, Physiologie, Funfter Band, s. 163.
[2] Pflüger's Archiv, Band xii., s. 288.
[3] Hoppe-Seyler, Phys. Chemie, s. 270.

Glands of Lieberkühn.

By far, however, the greatest quantity of the intestinal juice is secreted by the follicles of Lieberkühn, otherwise known as the simple tubular glands of the intestine. These glands resemble somewhat the pyloric tubules of the stomach, consisting of a basement membrane lined with a single layer of columnar cells, among which numerous goblet or mucin-producing cells occur. The tubules having a diameter of about $\frac{1}{14}$ of a millimeter ($\frac{1}{350}$ inch) extend through the mucous membrane, their blind ends looking towards the muscular coat, their mouths into the cavity of the intestine. The secretion of these tubules will therefore pass into the interior of the intestine. The tubules are as closely packed together as possible and are only absent in that part of the duodenum where the glands of Brunner are found, and in the remaining part of the small intestine, the Peyer's patches and solitary glands, and even here they are not entirely absent.

From the immense number of these tubules one would infer that a very considerable quantity of intestinal juice is secreted. The exact amount daily poured into the intestine has never been accurately determined; it does not appear to be, however, as much as we would have anticipated.

Methods of Obtaining Intestinal Juice.

Various experimental processes have been resorted to from time to time with the object of obtaining intestinal juice and of determining its composition and properties. Among the earlier methods may be mentioned that of withdrawing in a living animal a loop of intestines, ligating it in two places, replacing it for a while in the abdominal cavity, and then opening it, the fluid secreted in the meantime being assumed to be intestinal juice.[1] Another method consisted in cutting off the bile and pancreatic juices by ligating the bile and pancreatic ducts, the changes undergone by the food being attributed under such circumstances to the intestinal juice.[2] More recently another method of procedure has been adopted. This consists in completely excising a loop of intestine without injuring its nerves or blood vessels, suturing the cut ends of the alimentary canal, ligating one end of the excised loop and attaching the other to the abdominal wall so as to make a permanent fistula.[3] A later modification of the above method is to attach both ends of the excised loop to the abdominal wall, the intestinal fistula then presenting an entrance and an exit orifice.[4] The secretion [5] obtained from a dog, for example, by this method is of a yellow color, alkaline in reaction, and consists of water, albuminous principles, and

[1] Frerichs, Wagner Physiologie, 1846, Band III., s. 581.
[2] Bidder & Schmidt, Die Verdauungssäfte, 1852, s. 271.
[3] Thiry, Sitzberichte d. Wiener Akad., 1864, p. 77.
[4] Moleschott, Untersuch. zür Naturlehre, Band xiii., 1888, s. 40.
[5] Röhmann, Pflüger's Archiv, 1887, Band 41, s. 411.

salts. Among the latter may be mentioned sodium carbonate, to which the alkalinity of the secretion is due, and which, perhaps, aids also in the emulsification of the fats. The intestinal juice appears to act more particularly upon the carbohydrates, it containing enzymes, which convert starch into maltose, and the latter into glucose, and inverts cane sugar into levulose and glucose. It has little or no effect, however, upon proteids or fats. Although the method (Thiry-Vella) of obtaining intestinal juice from an animal, just described, is less objectionable than those formerly made use of, it is questionable, at least, whether the secretion so obtained was normal. Even admitting, however, that it was so, it does not follow that its properties would be necessarily the same as those of human intestinal juice.

Intestinal Juice in Man.—Indeed, what is positively known of the properties of the secretion in man has been learned rather from observations made upon intestinal fistulæ occurring in human beings as the result of wounds or operations, such as those described by Busch and Demant, than from experiments performed upon animals. The case of Busch,[1] just referred to was that of a woman thirty-one years of age, in the sixth month of her fourth pregnancy, being tossed by a bull, was wounded in the abdomen. The wound was situated between the umbilicus and pubes, and consisted of two contiguous openings communicating with the intestinal canal. It is probable that these two openings were in the upper third of the small intestine.

Notwithstanding her ravenous appetite the patient became very much emaciated in consequence of her food passing out of the upper of the two openings just referred to. It occurred to Busch, however, that the life of the woman might be saved by introducing cooked food into the lower opening, or that communicating with the lower portion of the intestine. This plan of treatment proved successful. The nutrition of the patient rapidly improved. The opening, however, not uniting, the woman was made the subject of the observations contained in the paper just referred to.

It will be observed that from the peculiar conditions of the case, food introduced by the mouth, unless absorbed by the stomach, would pass on into the upper portion of the intestine, and so out of the body by the upper of the two openings, having been modified in its course by the saliva, gastric, intestinal, and pancreatic juices, and the bile; whereas, food introduced into the lower of the two openings would be modified by the intestinal juice only, as it passed along the small intestine, and if not digested or absorbed would pass out by the anus unchanged. The conditions of the experiment were, therefore, perfectly physiological.

The intestinal juice was secreted in response to the natural stimulus of the food, while its effect upon the different kinds of food could be studied, either mixed or unmixed with the gastric, pancre-

[1] Virchow's Archiv, 1858, Band xiv., s. 140.

atic juices, etc. Necessarily, the quantity of intestinal juice obtained at any one time, by the introduction of sponges, etc., was not sufficient to admit of detailed analysis; the reaction was determined, however, to be alkaline. The general results of Busch's observations and experiments upon the intestinal juice may be summed up as follows:

Starch, both raw and hydrated, was invariably converted by it into maltose; cane sugar, however, was not changed into maltose, appearing in the feces as cane sugar. The intestinal juice digested more or less cooked meat and coagulated albumin, but had little or no effect upon fat; the latter when introduced into the lower opening of the intestine is always found in the feces as fat unchanged.

In the case of intestinal fistula lately observed by Demant,[1] starch was converted into maltose or glucose, but proteid substances did not appear to be transformed into peptone. No effect was observed upon neutral fats, though oily matters containing free acid were emulsified. The results of the observations of Demant confirm in the main those of Busch. It must be remembered, however, that the fistula in the former case was situated much lower than in the latter, and that the experiments upon the different kinds of foods were performed outside of the body after the intestinal juice had been drawn from the fistula. The observations of Busch were, therefore, made under more strictly physiological conditions than those of Demant, and deserve greater confidence.

It will be observed that while starch was converted into glucose, that fat was but little modified by the intestinal juice of either man or dog; that while proteid was digested at least in the woman, cane sugar was unaffected, whereas, proteid was undigested in the dog, but cane sugar was inverted into levulose and glucose. The fact that the cane sugar passed through the intestine of the woman with the fistula unaffected by the intestinal juice is important since cane sugar like maltose is unabsorbable. As such, either the amount of cane sugar converted into glucose in the stomach must be greater than is usually supposed, or the cane sugar must be transformed into glucose by some enzyme as it passes through the walls of the intestine, otherwise it will not be absorbed by the blood. That the latter is the case is rendered probable from the fact that cane sugar is converted into glucose by artificial intestinal juice. Basing our view more especially upon the case of intestinal fistula observed by Busch, it will be seen, that the action of the intestinal juice in digestion is of a supplementary character, reinforcing the effects of the saliva upon starch, and of the gastric juice upon the albuminoids, but having no effect, however, upon cane sugar or fat.

It should be mentioned in this connection, that, according to some chemists, intestinal juice possesses no digestive properties whatever, not acting at all upon carbohydrates or proteids and but to a limited extent upon fats. By such intestinal juice is regarded

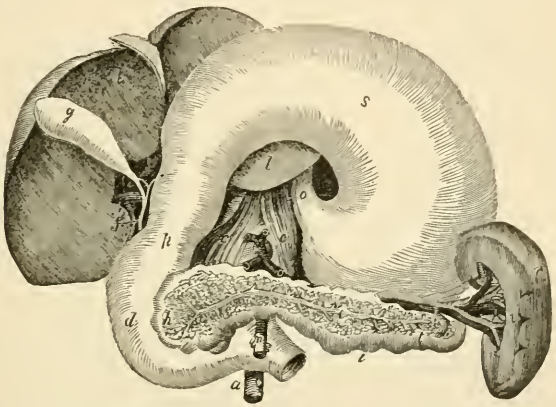
[1] Virchow, Archiv, 1879, Band lxxv., s. 419.

as being useful in neutralizing through its sodium carbonate the acid contents of the intestine derived from the stomach, and in promoting the emulsification of the fats.[1]

Pancreatic Juice.

The pancreas, in its general structure, resembles so closely the parotid and submaxillary glands that it was known to the older anatomists as the abdominal salivary gland (Fig. 39). It is situated

FIG. 39.



View of the pancreas and surrounding organs. ½. *l*. The under surface of the liver. *g*. Gall-bladder. *f*. The common bile-duct. *s*. The stomach. *d*. Duodenum. *h*. Head of the pancreas. *t*. Tail, and *i*, body of that gland. Pancreatic duct (*e*) and its branches. *r*. The spleen. *v*. The hilus. *c*, *c*. The crura of the diaphragm. (QUAIN.)

in the upper and posterior part of the abdominal cavity, behind the stomach and between the duodenum and the spleen. It is about 18 centimeters (7.2 inches) long, 4 centimeters (1.6 inches) broad, and 1.5 centimeters (0.6 inch) thick, and usually weighs about 75 grammes (2.6 ounces). The pancreas in its minute structure is a compound tubular gland, the lumen of each secreting tubule being continuous, as in the case of the salivary glands, with a system of capillaries lying between the secretory cells. In addition to the latter there occur also smaller cells ill-defined in shape, the so-called bodies of Langerhaus, which appear to be the early stages of the secreting cells. The duct of the pancreas (duct of Wirsung) running along the whole length of the gland opens into the duodenum along with the common bile duct, 8 to 10 centimeters (3 to 4 inches) below the pylorus. Not infrequently there is also a supplementary pancreatic duct (duct of Santorini) opening into the duodenum a little below the main duct.

[1] Bunge, op. cit., s. 186.

Methods of Obtaining Pancreatic Juice.

The first physiologist, so far as known to the author, who attempted to obtain the natural pancreatic juice from a living animal, was Regnerus de Graaf,[1] who, in 1662, opened the intestine of a dog and introduced a duck's quill into the orifice of the pancreatic duct. The fluid obtained by de Graaf was not however pancreatic juice, being acid in reaction, whereas the normal pancreatic juice is alkaline.

Although experiments were performed during the last century and the beginning of the present one little or nothing was learned of the functions of the pancreas till the epoch-making discoveries of Bernard[2] in 1846.

Bernard's method of obtaining the pancreatic juice consisted in opening the abdomen of a living dog and inserting a canula into the principal pancreatic duct. Bernard showed that during the intervals of digestion no pancreatic juice is secreted, and that the organ is of a pale color. The animal experimented upon should, therefore, be fed moderately an hour or so before the operation. The pancreas then becomes rose colored, full of blood, and secretes a viscid, alkaline juice, which flows into the duodenum, even before the digested food gets there from the stomach.

Further, Bernard determined in a general way the composition of the pancreatic juice in the dog and demonstrated its action upon starch, fat, and proteids. Bernard did not succeed, however, in establishing a permanent pancreatic fistula. Since then, however, this has been accomplished among others by Bernstein[3] and Heidenhain.[4] The method adopted by the latter of making a permanent pancreatic fistula consists in completely excising in an animal, a dog for example, that part of the duodenum, into which the main duct opens, and sewing it to the abdominal wall, the continuity of the intestine being restored by suturing its cut ends. By establishing such a fistula it can be shown that the flow of the pancreatic secretion begins as soon as food enters the stomach, the latter stimulating the gland to secrete, as we shall see hereafter, reflexly. The flow of the secretion usually attains a maximum during the first three hours after the taking of food. It then diminishes to the fifth or seventh hour, when it increases again, a second smaller maximum being reached about the eleventh hour. From that time on the flow diminishes until about the seventeenth hour when it ceases altogether.[5] The amount of pancreatic juice secreted in twenty-four hours has never been satisfactorily determined. It may be mentioned, however, that a permanent fistula yields far more pancreatic juice than a temporary one. The composition and specific

[1] Opera Omnia, 1678, p. 292. Memoire sur le Pancreas.
[2] Physiologie Experimentale, Tome ii., p. 180, Paris, 1856.
[3] Berichte d. Sächs, Ges. d. Wiss. Math.-phys. Cl., 1869, s. 96.
[4] Hermann, Handbuch, Fünfter Band, i. Theil, 1883, s. 178.
[5] Heidenhain, op. cit., s. 183.

gravity of the pancreatic juice varies like the amount according as it is obtained from a temporary or permanent fistula as shown by the

Composition of Pancreatic Juice of a Dog from a Temporary and Permanent Fistula.

	Collected on first opening the duct.[1]	Permanent Fistula.[2]
Water	900.8	979.0
Solids	99.2	20.0
Solids { Organic Matter	90.4	12.4
Solids { Inorganic "	8.8	7.6
The ash from 1000 parts of juice yielded—		
Soda	0.58	3.32
Sodic chloride	7.35	2.50
Potassic chloride	0.02	0.93
Phosphates of alkaline earths and iron	0.53	0.08
Sodic phosphate	.	0.01
Lime and magnesia	0.32	0.01

The pancreatic secretion from a temporary fistula is a clear, colorless, somewhat sirupy fluid with a strong alkaline reaction, due to the presence of sodium carbonate, and a specific gravity of 1030. The juice is rich in albumin, the latter coagulating like white of egg when heated and contains, in addition, three enzymes, a proteolytic one, trypsin, a diastatic one, amylopsin, and a fat-splitting one, steapsin, and possibly a fourth milk-curdling one. The mineral constituents consist of alkalines, chlorides and carbonates, phosphoric acid, lime, magnesia, and iron. The pancreatic secretion from a permanent fistula is a copious watery fluid, having a specific gravity of 1011, and containing less albumin and enzymes than that from a temporary one. The composition of human pancreatic juice is as yet but imperfectly known, the opportunity of collecting it being very rare. It may be mentioned, however, that according to Herter[3] the juice obtained in a case of stoppage of the duct was a clear, odorless, alkaline fluid, and contained the three enzymes. The pancreatic juice obtained from a young woman with pancreatic fistula following extirpation of a tumor of the pancreas consisted, according to Zawadsky,[4] in 100 parts, of water 86.4, organic substances 13.2. Of the latter, 9.2 parts were proteids, 0.3 salts. The juice transformed proteid into peptone, starch into maltose, and emulsified fats.

Formation of Pancreatic Juice.

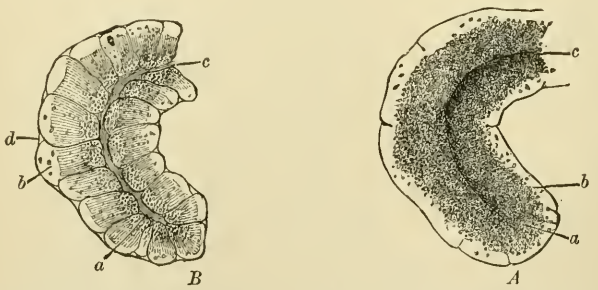
It has been learned from the researches of Heidenhain[5] more particularly, that each cell of the pancreas of a dog, for example,

[1] Bidder & Schmidt, Die Verdauungssäfte, 1852, s. 245.
[2] C. Schmidt, Ann. d. Chemie, xcii., 1854, s. 34.
[3] McKendrick, Physiology, Vol. 2, 1889, p. 125. Mandel, op. cit., p. 202.
[4] Centralblatt für Physiologie, Band v., 1891, s. 179.
[5] Heidenhain, op. cit., s. 188.

after a period of about thirty hours' fasting consists of two zones, an outer zone, which is either homogeneous or delicately striated and readily staining with carmine, and a large inner zone finely granulated and staining with difficulty; the nucleus, situated partly in the outer zone and partly in the inner one, being irregular in form. If the cell be examined, however, during a period of activity—six hours, for example, after food has been taken—the outer zone of the cell will be found to be the longest, the inner zone in some instances having disappeared altogether, and the whole cell will be seen to have become smaller and staining readily throughout almost its whole extent, through the small size of the inner zone, the nucleus being now regular in outline.

The natural inference to be drawn from these observations is, that during secretion the inner zone furnishes either the secretion or the materials of the same, and consequently diminishes in extent in proportion to the activity of the process, while the outer zone enlarges through assimilation of materials brought to the cell by the blood, and that the materials of the inner zone are elaborated at the expense of that of the outer one. That such is actually the case appears to have been shown by the observations of Kuhne and Lea,[1] made upon the pancreas of the living rabbit, in which the changes just described were observed as they took place (Fig. 40, *A*, *B*).

Fig. 40.



A portion of the pancreas of the rabbit, *A* at rest, *B* in a state of activity. *a*. The inner granular zone, which in *A* is larger, and more closely studded with granules, than in *B*, in which the granules are fewer and coarser. *b*. The outer transparent zone, small in *A*, larger in *B*, and in the latter marked with faint striæ. *c*. The lumen, very obvious in *B*, but indistinct in *A*. *d*. An indentation at the junction of two cells, seen in *B*, but not occurring in *A*. (Kuhne and Sheridan Lea.)

The fact that a glycerin extract made out of a pancreas taken out of the body while still warm has no digestive effect, whereas the same glycerin extract made out of a pancreas kept for twenty-four hours will digest fibrin, shows that the pancreas contains at the moment that it is taken out of the body but little trypsin, but that it does contain a substance, the so-called trypsinogen, readily converted into trypsin. If such be the case it would appear then that the trypsin, the active proteolytic enzyme or ferment of the pan-

[1] Verhandl. Nat. Hist. Med. Verein, N. F., Band 1, Heidelberg, 1877.

creatic juice, is developed out of the zymogen, trypsinogen, stored up in the inner zone of the cell, and that the latter is elaborated out of the materials of the outer zone. As to whether the other enzymes, the amylopsin and steapsin, are produced in the same way has not yet been positively established. In all probability, however, they are derived from mother substances or zymogens, which, if ever isolated, might be appropriately named amylopsinogen and steapsinogen. The pressure under which the pancreatic juice is stated[1] to be secreted is about 17 millimeters of mercury.

It has already been incidentally mentioned that pancreatic juice acts upon proteids, carbohydrates, and fats. This is due to the secretion containing, as we have just seen, three enzymes, trypsin, amylopsin, and steapsin, to the consideration of which let us now turn.

Action of Trypsin.—The chemical constitution of trypsin is unknown, it never having been isolated in a sufficiently pure state to admit of analysis. It is regarded as being an enzyme on account of its characteristic action upon proteid. Extracts containing trypsin can be prepared in various ways. The ordinary method is to mince the gland and to cover for some time with glycerin. The gland should be kept for a few hours before using, in order to ensure the conversion of trypsinogen into trypsin. By adding a 0.3 per cent. solution of sodium carbonate to a pancreatic extract an artificial pancreatic juice is obtained which suffices very well for the demonstration of the action of pancreatic juice upon proteids. As pancreatic juice decomposes very rapidly, differing in this respect from gastric juice, it is advisable to add to the artificial pancreatic juice a little thymol or chloroform. The action of trypsin is retarded by cold and accelerated by heat, 40° C. (104° F.), but is stopped at high temperatures, the enzyme being then entirely destroyed. Like other enzymes the action of trypsin is retarded by an accumulation of digestive products. Trypsin, like pepsin, converts proteid into peptone. Any proteid that passes through the stomach undigested into the intestine will, therefore, be converted there into peptone. The mode of action of trypsin differs, however, in many respects from that of pepsin. Trypsin acts best in alkaline media, though, to some extent, also in neutral and faintly acid ones. Proteids do not swell up under the action of trypsin before they are changed into peptone, but are eroded or eaten away. Tryptic differs still further from peptic digestion in that the proteid splits at once into deutero albumoses without passing through primary albumoses stages.[2] The most remarkable difference, however, between the action of pepsin and trypsin is that, while the action of pepsin is limited to the conversion of proteid into anti- and hemipeptone, that of trypsin carries the process a step further, hemipeptone being converted by the latter into leucin or amido-

[1] A. Henry & P. Wollheim, Pflüger's Archiv, Band xiv., s. 457.
[2] Neumeister, Lehrbuch der physiologischen Chemie, 1897, s. 246.

caproic acid, tyrosin or oxyphenyl-amido propionic acid, aspartic acid or amido-succinic acid, tryptophan, a body of unknown nature, lysatinin, etc.

The significance of the conversion of hemipeptone by the action of trypsin into leucin, tyrosin, etc., is far from apparent. If proteid be regarded as repairing the waste of the tissue its usefulness in this respect would be lessened by part of it being converted into leucin, tyrosin, etc., and on the supposition that it is a source of heat, less would be liberated by the oxidation of leucin, tyrosin, etc., than by the oxidation of proteid, the former bodies being of simpler chemical constitution. On the other hand, if leucin, tyrosin, on account of being amido acid, are considered in any way as antecedents of urea then that part of the proteid from which they are derived, usually regarded as so valuable, would appear to be only so much waste material. Trypsin converts albuminoids as well as proteids into peptones. Thus, gelatin, which frequently is transformed only into galactose by pepsin, is finally converted into gelatin-peptone by trypsin. The action of trypsin on other bodies is not well established. It appears, however, to dissolve elastic tissue, membrane of fat cells, cartilage, liver, etc., except the nuclei. Trypsin does not act upon carbohydrates or fats.

Action of Amylopsin.—The action of the diastatic ferment of the pancreatic juice, amylopsin, appears to be identical with that of the ptyalin of the saliva. Amylopsin acts, however, more energetically than ptyalin, converting raw starch at the temperature of the body almost at once into maltose and with but little dextrose or glucose. When it is borne in mind that starch constitutes about one-half of our daily food and that its conversion into maltose by ptyalin and intestinal juice is somewhat limited, the amylolytic function of the pancreatic juice will be seen to be a most important one. The chemical nature of amylopsin is not known. It is regarded as being an enzyme not only on account of its characteristic action upon starch, but from being affected by heat, etc., in the same manner as the other members of that class. Amylopsin does not appear to exert any inverting effect upon cane sugar.

Action of Steapsin.—Little is known of the nature of steapsin, the third enzyme of the pancreatic juice. It has never been isolated in a pure state, and is readily destroyed. It is regarded as being an enzyme on account more especially of its action upon fat, the latter, as we have seen,[1] under its influence taking up water and splitting into glycerin and the fatty acid of the particular fat used.

Tristearin.		Water.		Stearic acid.		Glycerin.
$C_{57}H_{110}O_6$	+	$3(H_2O)$	=	$3(C_{18}H_{36}O_2)$	+	$C_3H_8O_3$

This is a most important function, since the fatty acid so set free in combining with the alkali of the pancreatic and intestinal juices and of the bile forms soap, which will emulsify the fat, and thereby

[1] P. 53.

render it susceptible of absorption. It should be mentioned in this connection, in order to avoid misapprehension that in the emulsification of a given quantity of fat eaten, that only a fractional part (5 per cent.) is split into glycerin and fatty acid, the small quantity of soap formed from the latter sufficing to emulsify the rest of the fat, which remains neutral, and is absorbed as such. It may be mentioned in this connection that a fat is said to be emulsified when it is subdivided into very minute globules, which do not run together and which remain uniformly distributed throughout the medium in which they are present. That the emulsification of a neutral fat is due to the action of the soap formed through the splitting and subsequent saponification of a part of it can be shown in numerous ways. Among others the addition of a 0.3 per cent. solution of sodium carbonate to a slightly rancid oil, that is an oil containing a little free acid will produce at once a fine emulsion, due to the soap formed through the fatty acid combining with the alkali, whereas the addition of alkali to a perfectly pure oil will form no emulsion. It is difficult to say just why soap subdivides fat to the extent that obtains in a fine emulsion. If the minute globules, once formed, become, however, surrounded by a film of soap, as is supposed, that would account at least for them not coalescing. The emulsification of fat in the intestine through the action of steapsin and soap is well seen in a rabbit fed with oil. As the pancreatic duct opens in this animal into the intestine 30 centimeters (12 inches) below the opening of the bile duct, a favorable opportunity is presented of observing the effect of pancreatic juice upon fat unmixed with bile. In a rabbit so fed emulsified fat is only found to any extent in that part of the intestine and lymphatics below the opening of the pancreatic duct.

This observation not only suggested to Bernard the idea that the pancreatic juice emulsified the fat—that is, reduced it to a fine state of subdivision, and so rendered it absorbable—but was also the starting-point of his researches upon the functions of the pancreas generally. It has also been often shown that pancreatic juice as obtained from a fistula or artificially prepared when shaken with oil will produce at once a fine and permanent emulsion. While there is no doubt that fat is emulsified in the economy by the pancreatic juice in the manner just described, it is nevertheless well known that fat is more readily split into fatty acid and glycerin, with subsequent emulsification by a mixture of pancreatic juice and bile, than by the former alone. The bile, though not containing a fat-splitting enzyme, appears to aid in some way the action of the steapsin of the pancreatic juice, and promotes emulsification through its alkaline salts, being better fitted to combine with the fatty acid set free by the steapsin to form soap than the alkaline salts of the pancreatic juice itself. The further influence of the bile in promoting the emulsification and absorption of fats will be referred to again. In addition to the three enzymes just described, the pan-

creatic juice is said [1] to contain, at least in animals like the pig and certain herbivora, a fourth enzyme as yet unnamed, which causes the coagulation of neutral or alkaline milk.

Internal Secretion of Pancreas.

Recent experiments [2] have shown that extirpation of the pancreas in animals is followed by the appearance of sugar in the urine, even when no carbohydrate food is eaten. It is also well known that in certain cases, at least, diabetes mellitus in man is associated with disease of the pancreas. The glycosuria so produced is not due, however, as might be supposed, to suppression of the pancreatic juice since the ducts of the latter can be ligated or occluded without any sugar appearing in the urine. It has been inferred, therefore, that the pancreas produces an internal as well as an external secretion which contains possibly an enzyme, which, passing into the lymph and blood, promotes the combustion of sugar or prevents in some way its production by the liver or other organs.

Functions of the Liver.

The liver may be regarded as a compound tubular gland, the hepatic cells being disposed in each lobule, in columns radiating from the central vein, each cell being in contact on one side with a blood capillary and on the other with a bile duct. Indeed, the latter begin as interspaces between two adjoining hepatic cells, and as the biliary capillaries so formed become in time the interlobular biliary ducts, so the hepatic cells pass more or less abruptly into those lining the latter.

The Bile.

The bile is elaborated by the hepatic cells out of the materials supplied by the blood of the portal vein and hepatic artery. The bile is not, however, a mere filtrate, as its important constituents do not exist as such in the blood, but are produced by oxidation, etc., within the hepatic cells themselves. The pressure under which the bile is secreted is said to be equal to 15 mm. ($\frac{3}{5}$ of an inch) of mercury greater than that exerted by the blood of the portal vein. The bile appears to be secreted continuously within the hepatic cells, and, passing into the intercellular spaces or beginnings of the bile ducts, is transformed by the biliary ducts proper and the hepatic duct into the gall-bladder, where it is temporarily stored until it passes into the intestine. It appears, however, in cases of human beings with a biliary fistula that the bile, though secreted continuously in the hepatic cells, is ejected in spurts by the large bile ducts through the contractions of their muscular fibers. The relaxation of the orifice of the ductus choledecus and the flow of

[1] Hammarsten, op. cit., p. 210.

[2] Mehring u. Minkowski, Archiv für exper. Path. u. Phar., Band xxvi., 1890, s. 371. Minkowski, Ebenda, Band xxxi., 1893, s. 85.

the bile into the duodenum is intimately associated with the state of digestion, the flow being greatly accelerated, from 3 to 5 hours and from 13 to 15 hours after the taking of food. The amount of bile secreted is usually said to be influenced by the kind of food eaten, more being secreted upon a flesh-fat diet than upon a purely fat or vegetable one. Recent researches appear to show, however, that the flow of bile is not materially affected by the diet.[1] Draughts of water increase the flow, but diminish relatively the solids of the bile. The quantity of bile secreted by man in a given period can only be approximately determined. Judging from that obtained from a fistula, as much as 1344 grammes (48 oz.) may be secreted in 24 hours.[2]

The bile as obtained in cases of biliary fistulæ is clear, greenish, brownish-yellow, neutral in reaction, and of a specific gravity of 1.002. When mixed, however, with the secretion of the gall-bladder and bile ducts which appear to owe their properties to the presence of a nucleo-albumin, rather than to mucin,[3] the bile is more or less ropy in consistence, with an alkaline or neutral reaction. It has a faint odor, a bitter taste and a specific gravity of about 1.020, and bright golden-red in color, as is the case also in the bile of the omnivora and carnivora, that of the herbivora being, on the contrary, of a golden or bright green, the difference being due, as we shall see, to the relative amount in which the bile pigments, bilirubin and biliverdin, are present. It is oxidation of the latter which gives rise to the changes in color which the bile exhibits after exposure.

The bile when shaken up with air or water foams up into a frothy mixture. This property is due to the presence of the biliary salts. The bile is also dichroic—that is, it presents two different colors according to its mass, when examined with transmitted light; thus, while a layer of ox bile two or three centimeters thick is green, that of five or six centimeters appears red. The bile is also fluorescent; thus, if green bile be viewed by the violet or blue rays of the spectrum, it becomes faintly luminous, with a yellow, greenish tint.

The bile, chemically, is a highly complex fluid, consisting of water, biliary salts, mucus, pigment, cholesterin, fats, and inorganic salts, the water and solids being in 100 parts in the proportion of about 86 to 14.

Of the different principles which constitute the bile most of them pre-exist as such in the blood, the biliary acids and the biliary pigment are not found, however, in the latter, but are elaborated by the liver cells out of the principles brought to them by the blood.

The biliary salts do not consist, as one would suppose from their name, of simply inorganic salts, such as are ordinarily found in the

[1] Robson, Proc. Royal Society, Vol. 47, 1890, p. 507.
[2] Copeman, Journal of Physiology, Vol. x., 1889, p. 231.
[3] Hammarsten, op. cit., p. 145.

COMPOSITION OF THE BILE.[1]

	Frerichs.			Gorup Besanez.		
	Man, æt. 18.	Man, æt. 22.	Man, æt. 49.	Man, æt. 68.	Woman, æt. 28.	Boy, æt. 12.
Water	86.00	85.92	82.27	90.87	89.81	82.81
Solids	14.00	14.08	17.73	9.13	10.19	17.19
					5.65	
Biliary acids with alkali	7.22	9.14	10.79	7.37	....	14.80
Fat	0.32	0.92	4.73	....	3.09	
Cholesterin	0.16	0.26				
Mucus and pigment	2.66	2.98	2.21	1.76	1.45	2.39
Inorganic salts	0.65	0.77	1.08	....	0.63	

secretions, but of soda, united with glycocholic and taurocholic acids, the organic nitrogenized acids so characteristic of the bile, and upon which, to a great extent, the properties of the latter depend.

The biliary salts, the sodium taurocholate ($C_{26}H_{44}NSO_7Na$) and the sodium glycocholate ($C_{26}H_{42}NO_6Na$), may be obtained from the bile by appropriate means in the form of crystals.

FIG. 41.

Sodium glycocholate from ox bile, after two days' crystallization. At the lower part of the figure the crystals are melting into drops, from the evaporation of the ether and absorption of moisture. (DALTON.)

It is an interesting fact that the biliary salts, like glucose, lactose, and glycogen, exert a right-handed rotation on polarized light, all other substances in the animal body, so far as is known, having the opposite effect when examined by polarized light.

The biliary acids themselves may be separated from their respective salts by means of dilute sulphuric acid or lead acetate and sulphydric acid. The relation existing, chemically, between these two acids, is shown in the formula:

Taurocholic acid. Glycocholic acid.

$$C_{26}H_{45}NSO_7 - H_2O{-}S = C_{26}H_{43}NO_6$$

[1] Gorup Besanez, Lehrbuch der Physiologischen Chemie, 1878, s. 519. It should be mentioned in this connection that the later analyses of Trifanowski, Socoloff, and Hoppe-Seyler differ quantitatively somewhat from those given in the text.

by which it is seen that, in deducting water and sulphur, taurocholic becomes glycocholic acid. As a general rule, both the biliary acids are present in human bile, though the proportion in which they exist may vary considerably.

It has already been mentioned that the bile acids do not exist in the blood, but are elaborated in the liver. This has been shown by experiments performed upon animals. Thus, for example, after ligation of the choledechus duct, the bile acids pass into the lymph, and thence by the thoracic duct into the blood, whereas, if both ducts are ligated, no acids pass into the blood, which would not be the case if they were produced by any other organs than the liver. It has also been stated that in animals in which the liver has been extirpated, the bile acids do not accumulate in the blood or elsewhere, a further proof that they are elaborated by the liver.

Taurocholic and glycocholic acids when boiled with acids or alkalies take up water and split into cholalic acid and taurin and cholalic acid and glycin respectively, as shown by the following reactions:

$$\underset{\text{Taurocholic acid.}}{C_{26}H_{45}NSO_7} + \underset{\text{Water.}}{H_2O} = \underset{\text{Cholalic acid.}}{C_{24}H_{40}O_5} + \underset{\text{Taurin.}}{C_2H_7NSO_3}$$

$$\underset{\text{Glycocholic acid.}}{C_{26}H_{43}NO_6} + \underset{\text{Water.}}{H_2O} = \underset{\text{Cholalic acid.}}{C_{24}H_{40}O_5} + \underset{\text{Glycin.}}{C_2H_5NO_2}$$

While cholalic acid is a non-nitrogenous acid and derived, therefore, possibly from sugar or fat, it is associated in both the above cases with nitrogenous bodies derived from proteid, taurin or amido-ethyl sulphonic acid, and glycin or amido-acetic acid. The reactions just given are especially interesting as it has been shown that the biliary acids split in a similar manner in the intestine into taurin, glycin, and cholalic acid. While the further fate of these substances is perhaps not perfectly understood, it appears probable that they are partly reabsorbed by the blood and partly voided, the dyslysin ($C_{24}H_{36}O_3$) occurring in the feces, being dehydrated cholalic acid.[1] The presence of bile acids is usually shown by the well-known Pettenkofer's test. This test depends upon the fact that when sulphuric acid is added to cane sugar, a substance, furfurol, is formed which is acted upon by the biliary acids in such a manner that the liquid assumes a beautiful cherry-red or red-violet color. Pettenkofer's test is usually performed in the following manner: One part of cane sugar being dissolved in four parts of water, one drop of the solution is added to every cubic centimeter of the solution to be examined. To this mixture a few drops of sulphuric acid are slowly added, the temperature of the mixture not being allowed to rise above 70° C. (158° F.). If bile acids be present in pro-

[1] To avoid misunderstanding, it may be mentioned that there are different kinds of cholalic acid, one variety known as choleic acid, occurring in ox bile, another, fellic acid, in human bile, etc. Indeed, recent to the recent observations of Lassar Cohn, Zeitschr. für Phys. Chemie, Band 19, 1894, s. 570, it appears that both these acids are found in human bile and even in greater quantity than cholalic acid proper.

portions of 1 to 500 in a solution treated this way, a cherry-red color first appears, which rapidly changes to violet, and then to a deep red purple. Inasmuch, however, as there are other substances, such as albuminous matters, amylic alcohol, olein, morphine, codeine, etc., which present this same play of colors when treated with cane sugar and sulphuric acid, it is necessary to point out the precautions which must be taken in applying Pettenkofer's test for bile, in order to exclude these sources of error. With the exception of the morphine, which is unlikely to occur in an extract of the animal fluid, especially in the proportions just referred to, this can be accomplished if the suspected liquid be first evaporated to dryness, the dry residue extracted with absolute alcohol and decolorized, if necessary, with animal charcoal, then precipitated with ether, and the precipitate dissolved in water. Spectrum analysis of Pettenkofer's test can also be used in distinguishing bile from the substances just referred to, and which give the same reactions.

Pettenkofer's test, when carefully applied, is an extremely delicate one, since a solution of sodium glycocholate in the proportion of 1 to 2000, and sodium taurocholate of 1 to 3000 of water respectively, can be recognized by it.

Bile Pigments.

The color of the bile, as we have already mentioned, depends upon the proportion in which the bile pigments, bilirubin and biliverdin, are present. Bilirubin ($C_{16}H_{18}N_2O_3$), the red or orange-red coloring matter of the bile, can be obtained from gall stones by extraction, is crystallizable, readily soluble in alkaline liquids and chloroform, less so in alcohol and ether, but entirely insoluble in pure water. If to a solution of bilirubin, spread out on the surface of a porcelain plate, for example, a drop of nitrous nitric acid be added, a characteristic play of colors—green, blue, violet, red, and, finally, yellow—will be observed at the circumference of the drop of acid as it diffuses itself through the solution, and which is due to the successive oxidation of the bilirubin. This reaction is an exceedingly delicate one, the play of colors being evident in solutions of bilirubin containing only 1 part in 80,000, and is, therefore, utilized as Gmelin's test in determining the presence of the bile pigments. Bilirubin, though found as hæmatoidin in blood extravasations and apoplectic clots in different parts of the body, appears to be normally elaborated by the hepatic cells out of the hæmatin or the coloring matter of disintegrated red blood corpuscles, the process being apparently one of hydration with subsequent splitting off of iron.

$$\underset{\text{Hæmatin.}}{C_{32}H_{32}N_4O_4Fe} + \underset{\text{Water.}}{2H_2O} - \underset{\text{Iron.}}{Fe} = \underset{\text{Bilirubin.}}{2C_{16}H_{18}N_2O_3}$$

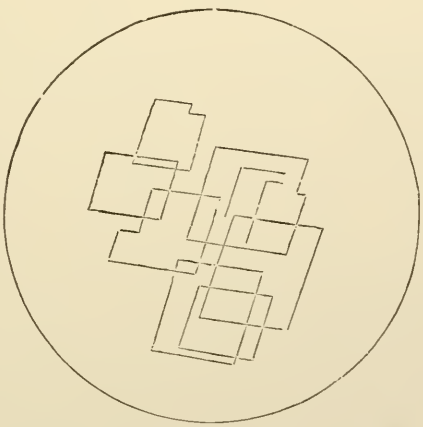
As a confirmation of the view that a genetic relation exists between bilirubin and hæmatin it may be mentioned that in Amphioxus

and the invertebrata in which red blood corpuscles do not occur in the blood, bile pigments are not found in the bile, and that the intravenous injection of hæmoglobin or of substances, like water, which disintegrate the red blood corpuscles, increase the bile pigments. Of the iron that separates from the hæmatin in the formation of bilirubin the greater part appears to be used again in the reformation of hæmatin, the remaining part being secreted in the bile. Bilirubin, through oxidation, as in the first stage of Gmelin's test, loses its red color and becomes green, being transformed into bile verdin ($C_{32}H_{36}N_4O_8$), the green-colored pigment of the bile.

Biliverdin crystallizes somewhat imperfectly from an evaporated solution in glacial acetic acid, is insoluble in water, ether, and chloroform, but is readily soluble in alkaline solutions and alcohol. It frequently constitutes an ingredient of human gall stones. Its presence can not only be determined by Gmelin's test, but by means of spectrum analysis.

Both bilirubin and biliverdin pass as the coloring matters of the bile into the alimentary canal from which they are partly absorbed and partly transformed by putrefactive processes into hydrobilirubin ($C_{32}H_{40}N_4O_7$), constantly found as one of the coloring matters of the feces, and is probably identical with the urobilin, the urinary pigment.

FIG. 42.



Cholesterin, from an encysted tumor. (DALTON.)

Cholesterin.—Cholesterin ($C_{26}H_{44}O$), so-called on account of its having been first obtained as a solid deposit from the bile, is a constant ingredient of that fluid occurring in the proportion of from one to three per cent. Cholesterin is usually regarded as being a monatomic alcohol, its chemical constitution being expressed by the formula $C_{26}H_{43}OH$. It is a crystallizable body appearing as thin, colorless, transparent, rhomboidal plates, usually with an ob-

long piece cut out of the corner (Fig. 42) when deposited from its ethereal or alcoholic solution. Cholesterin is held in solution in the bile by the bile acids, being insoluble in water and dilute saline fluids.

Cholesterin is found in the blood, spleen, nervous system, etc. It differs, therefore, from the bile acids and pigments, in that it is not elaborated by the liver, but is simply separated from the blood by the latter, whence it passes as a constituent of the bile into the alimentary canal, and is excreted in the feces apparently unchanged. The bile contains, in addition to the bile acids, pigments, and cholesterin, small quantities of neutral fats, soaps, lecithin, and urea. Among the inorganic constituents of the bile may be mentioned sodium chloride, calcium and magnesium phosphate, and iron. The gases of the bile consist principally of carbon dioxide with a small quantity of nitrogen and traces of oxygen.

Functions of the Bile.—It was long since inferred by Haller[1] from the fact of the bile passing into the upper rather than the lower part of the intestine that it plays some important part in digestion. That such is the case is shown by the fact that in cases of biliary fistula, far less fat is absorbed by the lymphatics of the small intestine than in the normal condition, the bile aiding the pancreatic juice in splitting and emulsifying the fats and promoting their subsequent absorption. Indeed, according to some observers, emulsification of the fats does not take place in the absence of the bile.[2] This important function of the bile appears to be due to its bile acids, although the exact manner in which they act in this respect is not, as yet, clearly understood. Bile appears to have also a slight diastatic action. On the other hand, the bile must be regarded as an excretion as well as a secretion, since part, at least, of the bile acids and pigments, the cholesterin and lecithin, are excreted in the feces.[3] As bile promotes the onward movement of the contents of the alimentary canal, it is usually regarded as being a natural purgative. It is well known that in cases of biliary fistula or occlusion of the bile ducts that when fat or meat is eaten the feces become very offensive, and from this reason it has been inferred that the bile is an antiseptic. While bile undoubtedly retards in some way putrefaction, its action in this respect does not appear to be directly antiseptic, as bile itself outside of the body putrefies rapidly. In conclusion, it may be mentioned that peptic digestion is brought to a standstill in the intestine through the acid chyme of the stomach being neutralized or made alkaline through admixture with the pancreatic juice and the bile, the pepsin being carried down with the precipitate formed by the mixture of chyme and bile and which consists partly of proteids and partly of bile acids.

[1] Elementa Physiologie, Tomus sextus, p. 615.
[2] Dastre, Comptes Rendus, Soc. Biol., 1887, p. 782.
[3] See p. 22.

Origin and Function of Glycogen.

The liver, as might be inferred from its size, possesses other functions than that of merely elaborating bile, one of the most important of which is the production of glycogen. Glycogen $(C_6H_{10}O_5)_6$ is isomeric with starch and dextrin. It differs, however, physically from the latter in that its solution is opalescent, while that of dextrin is clear, and that the addition of iodine gives to the solution of glycogen a deep brownish-red color, but to that of dextrin a rosy red, and to starch the characteristic blue. The presence of glycogen in the cells of the liver is usually shown by the iodine reaction just referred to, the organ having been removed about twelve hours after a meal and hardened in alcohol. Glycogen is soluble in both hot and cold water, but insoluble in ether and alcohol, and is one of the few substances in the animal body that deviate the plane of polarization to the right. Glycogen in solution, like other starchy bodies, is readily converted into glucose when boiled, for example, with a dilute mineral acid, or brought in contact at the temperature of the body with saliva, pancreatic or intestinal juice, or serum. Glycogen becomes glucose also, if simply allowed to remain in the liver after death, or if brought in contact with its tissue after removal from the body, the phenomenon being essentially one of hydration, as shown by the formula

$$\underset{\text{Glycogen.}}{C_6H_{10}O_5} + \underset{\text{Water.}}{H_2O} = \underset{\text{Glucose.}}{C_6H_{12}O_6}$$

Glycogen can be readily obtained in the following manner: Immediately after death, the liver of a well-fed animal is taken out of the body and cut up into small pieces, and coagulated with boiling water. A concentrated decoction is then made of the liver tissue thoroughly ground up, and decolorized with animal charcoal. Strong alcohol being now added, the glycogen will be precipitated as a white powder; but this is impure, being mixed with a small quantity of glucose, biliary salts, and albuminous matter. The latter can be removed, however, by washing with alcohol, and boiling with potassium hydrate. The residue being filtered and dissolved in water, and any albuminous principles still present being removed with acetic acid, the glycogen is reprecipitated with alcohol, and then dried, when it can be kept for a long time, it retaining its properties indefinitely. The quantity of glycogen in the liver may amount in man to as much as ten per cent.—that is to say, assuming that the liver in man weighs about 1400 grammes (50 ounces), the glycogen present would be 240 grammes (5 ounces), the amount depending, however, upon the length of time elapsing since the taking of food, and the character of the latter, increasing with digestion and diminishing with fasting, and disappearing altogether if no food be taken for four or five days, being more abundant on a vegetable than on an animal diet, and particularly abundant if the food consists largely of carbohydrate matter. When the chemical

composition of glucose and glycogen is compared, and when it is remembered that all of the starch and sugar of the food are transformed into glucose during digestion, the above becomes intelligible, on the supposition that the glucose carried by the portal vein to the liver during absorption is converted by and stored up in the liver cells as glycogen, the transformation of the glucose into glycogen being one of dehydration, as shown by the formula:

$$\overset{\text{Glucose.}}{C_6H_{12}O_6} - \overset{\text{Water.}}{H_2O} = \overset{\text{Glycogen.}}{C_6H_{10}O_5}$$

The fact of glycogen being developed on an animal diet as well as on a vegetable one, though in less amount, so far from being an objection to the origin of glycogen, as just offered, is a confirmation of it, since it is readily conceivable how nitrogenized matter like glycin may, for example, split up in the economy into glucose and urea, as shown by the formula:

$$\overset{\text{Glycin.}}{4(C_2H_5NO_2)} = \overset{\text{Urea.}}{2CON_2H_4} + \overset{\text{Glucose.}}{C_6H_{12}O_6}$$

the glucose becoming then glycogen, as when derived from vegetable matter, and the urea being eliminated by the kidneys. That such a transformation of nitrogenized matter actually takes place in the system, at least under certain conditions, appears from the fact that in certain cases of diabetes,[1] when the food contained no carbohydrate matter, the glucose increased *pari passu* with the urea. The above, to a certain extent theoretical, considerations are confirmed by experimental ones. Thus it has been shown by Bernard,[2] Pavy,[3] Doch,[4] Tscherinow,[5] and others that the amount of glycogen in the liver is notably increased within a few hours after the taking of starchy or saccharine articles of food, and that while glycogen is developed on an animal diet, the amount produced is far less than on a vegetable one. Glycerin increases the amount of glycogen but it appears to do so only indirectly by interfering in some way with its reconversion into glucose by the liver cells. Fat does not influence the production of glycogen.

There appears to be no doubt, therefore, that the carbohydrate and nitrogenized principles in part of the food being transformed into glucose are conveyed in the blood of the portal vein to the liver, and that the glucose so derived is, probably by dehydration, converted into glycogen, and, for the time being, at least, is stored up as such in the liver cells. That the glycogen remains, however, only temporarily in the liver, appears from the fact, as shown first by Bernard,[6] that in a fasting animal, or in one that has been fed

[1] Singer, Med. Chir. Trans., xliii., p. 327.
[2] Physiologie Experimentale, p. 159. Paris, 1855.
[3] Nature and Treatment of Diabetes. London, 1862.
[4] Pflüger's Archiv, 1872, Band v., s. 571.
[5] Virchow's Archiv, 1869, Band xlvii., s. 102.
[6] Op. cit., p. 204.

on an exclusively meat diet, that the liver and the blood of the hepatic vein contain glucose, though there is not the slightest trace of it in that of the portal vein, the glycogen stored up in the liver during the intervals of digestion being gradually converted into glucose, and conveyed away by the hepatic veins into the general circulation.

That the transformation of glycogen into glucose is merely a question of time, is shown by the fact that a decoction made out of a liver taken out of the body of a fasting animal is clear, whereas if it is made out of one taken from an animal fed within a few hours, it is decidedly opalescent through the glycogen it contains not as yet having been transformed into glucose.

It is denied by some experimenters that the liver actually contains glucose during life. Inasmuch, however, as glucose can be demonstrated in the liver within twenty seconds after the death of the animal from which it has been taken, it can hardly be doubted that such is the case. While there may be a difference of opinion as to whether the liver contains glucose during life, there is no difference of opinion as to its containing glucose after death. Indeed, if all the blood be washed out of the liver by forcing water through the portal vein, the liquid, as it escapes by the hepatic vein, will be found to contain glucose, and this even upward of half an hour after repeated injections. And then, when the presence of glucose can no longer be demonstrated, if the liver be put aside in a warm place for a few hours, glucose can again be obtained, it being a long time before its glycogen, the source of the glucose, is exhausted.

The conversion of glucose into glycogen, and the storage of the latter in the liver is of advantage to the economy, since the sugar produced during digestion would otherwise accumulate to such an amount in the blood that it would be excreted by the kidneys and therefore wasted. On the other hand, as the sugar of the blood is diminished in amount the loss is made good by the reconversion of the glycogen into glucose and the passage of the latter into the blood. The principal use of glycogen appears, therefore, to depend upon the readiness with which it is developed out of glucose and reconverted into the same, the sugar of the blood being thereby maintained in normal amount. Glycogen occurs not only in the liver but in the muscles, placenta, brain, and other parts of the body as well. The glycogen of muscle is usually regarded as so much stored up carbohydrate material, which can be readily converted into glucose and in being oxidized will liberate energy. As a confirmation of this view it may be mentioned that the glycogen of both muscles and liver is rapidly used up by muscular exercise unless food is supplied.

In conclusion, it may be pointed out that the transformation of glucose into glycogen, and of glycogen into glucose in the animal, finds an analogy in the vegetable, since, as is well known, the

starch in the leaves of a plant having been converted into sugar, passes down to the roots, where not infrequently it is reconverted into starch.

Production of Urea by the Liver.

One of the most important functions of the liver, to a considerable extent at least, is the production of urea. Urea (CH_4N_2O) is usually regarded as being a carbamide or an amide of carbon dioxide, $CO<\begin{matrix}NH_2\\NH_2\end{matrix}$, that is, CO_2, in which an atom of oxygen is replaced by the residues of two molecules of ammonia. Such being its chemical constitution, its production by the liver can be readily accounted for on the supposition that the leucin, tyrosin, and other amides developed in the digestion of proteid food stuffs are transformed into ammonium carbamate, which being carried to the liver is there dehydrated, and becomes urea.

Ammonium carbamate.		Water.		Urea.
$CO<\begin{matrix}NH_2\\ONH_4\end{matrix}$	—	H_2O	=	$CO<\begin{matrix}NH_2\\NH_2\end{matrix}$

While there may be some doubt as to whether urea is produced in exactly this way in the liver, recent experiments prove conclusively that urea is produced in the liver in some such way. Thus, for example, according to Schröder,[1] when blood obtained from a well-fed dog was passed through the blood vessels of the liver of another recently killed dog a noticeable increase in the amount of urea was observed, whereas when the blood used was obtained from a fasting animal there was no increase of urea. It was shown also by the same experimenter that the addition of ammonium carbonate to the blood circulating through the liver increased the amount of urea. This result can be explained by supposing that the ammonium carbonate becomes ammonium carbamate and then urea, or urea directly by dehydration, as follows:

Ammonium carbonate.		Water.		Urea.
$(NH_4)_2CO_3$	—	$2H_2O$	=	CON_2H_4

On the other hand it has been shown[2] in cases of animals in which the blood of the portal vein has been made to pass directly into the vena cava without going through the liver at all that carbamates appear in the blood and that the amount of urea diminishes notably, carbamates not being converted into urea in the absence of the liver. Among its other functions the liver performs the important one of removing and retaining heterogeneous bodies from the blood, or of rendering such as are of a poisonous nature innoxious. Thus, for example, while salts of copper are retained by the

[1] Archiv für exper. Path. u. Phar., 1882, Band xv., s. 364; 1885, Band xix., s. 373.

[2] Hahn, Pawlow, Massen, and Nencki, Archiv für exper. Path. u. Phar., 1893, Band xxxii., s. 161.

liver, alkaloids such as phenol and cresol, poisonous aromatic substances derived from the putrefaction of proteid food in the intestine, are converted into the harmless ethereal or conjugate sulphates and which, passing into the general circulation, are excreted by the kidneys. By a similar synthesis, indol and skatol, also putrefactive products, after being converted by oxidation into indoxyl and skatoxyl are transformed by the liver into the corresponding ethereal sulphuric acids, indoxyl-sulphuric acid (indican) and skatoxyl sulphuric acid, and pass in that form into the urine.

Putrefactive Processes in the Intestines Caused by Micro-organisms.

It is well known that various kinds of micro-organisms are introduced into the alimentary canal with the food and drink which cause fermentation and putrefaction with the evolution of hydrogen, carbon dioxide, marsh gas,[1] sulphuretted hydrogen. Thus, for example, bacilli occur which, acting upon the carbohydrates, produce acetic, lactic, butyric acids, etc., or upon proteids breaking them up into leucin, tyrosin, cresol, phenol and its derivatives indol, skatol, fatty acids, etc. Organized ferments, fungi, are present, which appear to transform starch into glucose, cane sugar into glucose and levulose, and split fat into fatty acid and glycerin. It has already been mentioned that many micro-organisms are destroyed by the acid of the gastric juice, and it might be supposed, therefore, as the reaction of the intestinal secretions is alkaline, that the small intestine would present conditions favorable for fermentation and putrefaction. Recent observations[1] made upon cases of fistula of the ileum in human beings show, however, that upon a mixed diet while acetic and other acids are produced by the bactericidal fermentation of the carbohydrates, the products of the putrefaction of proteid are not developed, putrefaction being prevented from the presence of these acids. In the large intestine the alkali secreted being usually more than sufficient to neutralize the acid derived from the fermentation of the carbohydrates, the reaction of its contents is alkaline, and such proteid as has escaped digestion and absorption undergoes, therefore, putrefaction.

The Large Intestine.

This portion of the alimentary canal is so called on account of its relatively large size. It measures usually in length from 1.2 to 1.5 meters (5 to 6 feet), and in diameter from 3.7 to 7.5 centi-

[1] Marsh gas, light carburetted hydrogen or methane (CH_4), the only hydrocarbon found in the body, appears to be developed in the intestine from cellulose, according to the following reaction

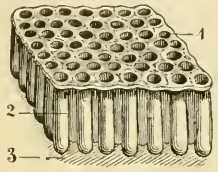
Cellulose.		Water.		Methane.	Carbon dioxide.
$C_6H_{10}O_5$	+	H_2O	=	$3CH_4$	+ $3CO_2$

[2] Macfadyen, Nencki u. Sieber, Archiv für exper. Path. u. Phar., 1891, Band 28, s. 311. M. Jakowski, Archives Des Sciences Biologiques, St. Petersburg, 1892, Tome I., p. 539.

meters (1.5 to 3 inches). The general direction of the large intestine beginning with the cæcum, is from the right iliac fossa upward, then transversely across to the left side of the body; thence downward into the left iliac fossa, finally terminating as the rectum. The small intestine is thus surrounded by the large intestine, the latter being disposed in the form of a horseshoe.

The large intestine, like the small, consists essentially of two coats, a mucous, including the submucous, and a muscular. In addition, the large intestine is, to a great extent, covered with peritoneum, which serves to maintain it in position, and to connect it with certain of the abdominal and pelvic viscera. While the villi and valvulæ conniventes are absent in the large intestine, throughout the whole extent of its mucous membrane there are found tubular and solitary glands which do not differ essentially in their minute structure from those of the small intestine. The tubular glands (Fig. 43) of the large intestine are, however, more numerous, longer, and more closely set together than those of the latter, and often are subdivided at their cæcal extremities.

Fig. 43.



Section of the mucous membrane of the colon. 1. Free surface exhibiting the orifices of the tubular glands, 2. 3. Fibrous tissue moderately magnified.

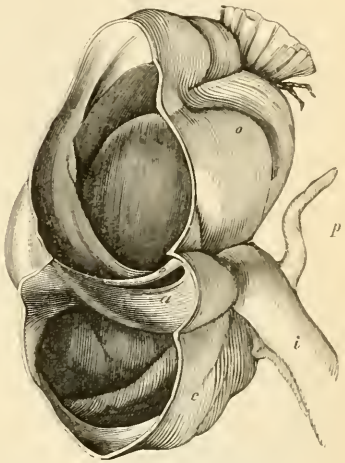
The mucous membrane of the large intestine is paler, thicker, and more closely adherent to the underlying parts than that of the small intestine. The muscular coat of the large intestine differs considerably in certain points from that of the small intestine. Thus, in the colon more particularly, the longitudinal fibers are gathered together in three well-marked bands, one of which is anterior, while the other two are latero-posteriorly situated. The large intestine is divided by anatomists into three portions, the cæcum, colon, and rectum, these differing in their size, shape, and the character of their mucous and muscular coats.

The most important part, physiologically, of the cæcum or caput coli, the widest portion of the large intestine, is the ileo-cæcal valve, by means of which the contents of the ileum, after they have passed into the large intestine, are prevented from returning into the small intestine. The small intestine opens into the large intestine by a slit-like aperture (Fig. 44, *a c*) which lies nearly transverse to the direction of the latter. This aperture is bounded above and below by two semilunar folds or valves which project inward toward the cæcum and colon. At each end of the aperture the two valves or folds run into each other and are then prolonged at each side as a ridge or frænum, which gradually fades away. That portion of the valve which looks toward the ileum is covered with villi, and in other respects resembles the mucous membrane of the small intestine, while that upon the opposite side of the valve is destitute of villi, and its mucous membrane is like that of the large intestine. Each segment of the valve is covered with mucous membrane, and

consists of submucous tissue and muscular fibers, derived from the circular muscular fibers of both the ileum and large intestine.

The longitudinal muscular fibers of the ileum, however, run continuously into those of the large intestine, taking no part in the formation of the valve, but are stretched across it. The effect of distention of the cæcum by its contents is that the frænа being put on the stretch, the edges of the valves are brought in apposition, closing the ileo-cæcal aperture so completely that all reflux from the large intestine into the ileum is prevented, but at the same time no hindrance is offered to the passage of the contents of the ileum into the large intestine. An interesting feature about the cæcum is its vermiform appendix (Fig. 44, *p*), a worm-like tube, beginning at its lower end and terminating in a blind extremity, attaining usually about a length of from 7.5 to 15 centimeters (3 to 6 inches), and having a diameter about the size of a quill.

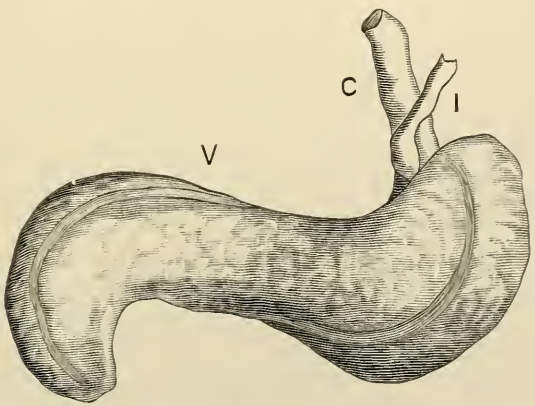
Fig. 44.



View of the ileo-colic valve from the large intestine. The figure shows the lowest part of the ileum, *i*, joining the cæcum, *c*, and the ascending colon, *o*, which have been opened anteriorly, so as to display the ileo-colic valve; *a*, the lower, and *e*, the upper segment of the valve. *p*. Vermiform appendix.

The vermiform appendix, so far as is known, has no use in man, but is a very interesting structure as representing in man, in a ru-

Fig. 45.

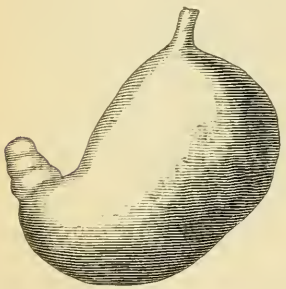


Cæcum of capybara. (From nature.)

dimentary condition, that which is well developed and performs important functions in many animals. Thus in the horse, tapir,

elephant, rabbit, and beaver, the cæcum is very large ; in the capybara (Hydrochærus), a species of rodent, the cæcum (Fig. 45, V) measured 65 centimeters (26 inches) in length, while in a koala (Phascolaretos), a small marsupial, also examined by the author, it attained a length of 125 centimeters (50 inches). Now, by comparing the cæcum in the capybara with the vermiform appendix in man, it will be found that the latter corresponds to the blind part of the cæcum, V, in the capybara, while the cæcum, or caput coli, in man is homologous with that part of the cæcum in the capybara communicating with the large intestine, I. In other words, the cæcum in the animals just mentioned is equal in man to the vermiform appendix and cæcum. Further, it will be observed that the cæcum of the capybara (Fig. 45) is much longer than the stomach of that animal (Fig. 46), the latter measuring only 25 centimeters (10 inches), while it is needless to state that just the reverse relation obtains as regards the same parts in man. The significance of this contrast is evident enough when the digestion of food in man and the capybara is considered. In the first instance, as we have seen, the action of the stomach is very important ; in the latter instance it is but relatively so, the imperfect digestion of food in the stomach of the capybara being completed in its cæcum.

Fig. 46.



Stomach of capybara. (From nature.)

In the same manner the cæcum in the tapir, horse, and elephant, etc., supplements the imperfect digestive action of the stomach in these animals. On the other hand, in the giraffe, in which there are four well-developed stomachs, the cæcum is relatively small. In a word, there is an inverse ratio, both anatomically and physiologically, between the stomach and the cæcum ; when the one is large and active, the other is small and inactive, and *vice versa*. The conclusion must not, however, be drawn that the cæcum in these animals secretes a gastric, or any other digestive juice. The cæcum rather appears to be a receptacle where the fluids absorbed by the food in its rapid passage through the alimentary canal have time to produce their digestive effects.

The acid reaction often noticed in the cæcum of animals, and sometimes in man, is not due to acid secretion, but, as we have seen, to a kind of lactic or butyric acid fermentation set up in the food, the normal reaction of the secretion of the cæcum being alkaline. That the vermiform appendix in man is a rudimentary organ is confirmed by the fact that it is relatively longer in the embryo than the adult. It is worthy of note that the vermiform appendix is found as in man in all four anthropoid apes, the gorilla, chimpanzee, orang, and gibbon ; and more remarkable still that it is present in a marsupial, the wombat (Phascolomys).

In addition to what has already been said of the colon, an important feature is its sigmoid flexure, so called from the S-like curve the colon makes just before passing into the rectum. This curvature, as we shall see, is the position where the feces are temporarily retained.

The large intestine terminates in the rectum, which, while straight in animals in which it was originally described, is far from being such in man. In fact, the rectum in man first passes obliquely downward from left to right, from opposite the left sacro-iliac articulation to the middle line of the sacrum. It then curves forward back of the prostate in the male, and the vagina in the female, and finally passes backward and downward, terminating in the anus. The anus is a dilatable orifice, lined with mucous membrane and covered with skin, the skin and mucous membrane becoming continuous with each other. The margin of the anus and lower part of the rectum are embraced by the external and internal sphincter muscles, the levators ani and coccygei. These muscles serve to support the bowel, and to close its anal orifice. The internal sphincter muscle consists of the circular fibers only greatly developed. It is situated 2.5 centimeters (1 inch) above the anus, extending over 12 millimeters (about $\frac{1}{2}$ inch) of the intestine, and is about 4 millimeters (2 lines) thick.

The rectum, 20 centimeters (about 8 inches) in length, is not sacculated like the rest of the large intestine, the longitudinal muscular fibers being scattered over its surface. While the upper part of the rectum is narrow, at the lower part it is dilated into a kind of reservoir just above the anus. The mucous membrane of the rectum is more vascular, thicker, and redder than that of the colon, and moves more freely over the muscular coat. It is thrown into numerous folds, most of which are, however, effaced when the rectum is distended.

The Contents of the Large Intestine.—While there is no reason to suppose that anything like true digestion takes place in the large intestine of man, various important changes are effected there by which the undigested residue of the food is transformed into the feces, the most marked changes being in the consistence, color, and odor, and which are gradually developed as it passes from the cæcum through the colon into the rectum. As the undigested food passes through the large intestine its liquid portions are being constantly absorbed, the feces, therefore, have a much firmer consistence than the contents of the ileum. The large intestine is, therefore, physiologically important, as presenting an extensive absorbing, if not a digestive surface. The absorbing power of the rectum is well known. Indeed, life can be sustained for months by giving nutritious enemata.

The color of the feces is of a dark yellowish-brown, and appears to be due to the presence of stercobilin, the latter being either identical with or a derivative of hydrobilirubin. It is well known that

when the bile is deficient or absent, the stools become lighter or clay-colored. The color of the feces varies also according to the diet.

While the cause of the odor of the feces cannot be said to be exactly understood, there can be no doubt that it is due to a great extent to the skatol and indol which have escaped absorption, to the decomposition of the bile, and to the secretion of the glands of the colon and rectum.

The reaction of the feces is variable, sometimes acid, often alkaline or neutral, depending chiefly upon the kind of food eaten.

The entire quantity of feces passed in twenty-four hours upon a mixed diet amounts usually to from 120–150 grammes (4–5 ounces), but on a vegetable diet to as much as 333 grammes (11 ounces), which is, as might be expected, the vegetable diet containing so much indigestible matter. When the contents of the large intestine are examined microscopically, there will be found a number of undigested substances derived from the vegetable and animal foods. Among other matters, the spiral vessels of vegetables, the cortex of grains, hard vegetable seeds, structures generally consisting largely of cellulose, muscular tissue in various stages of disintegration, tendinous and elastic structure, the organic constituents of bone.

The feces chemically may be said to consist of seventy-five parts of water to twenty-five of solid residue. In the latter there have been found among other substances the ammonium-magnesium phosphate, the magnesium phosphate, salts of sodium, potassium, calcium, iron, fatty acids, excretin. The feces contain also mucous pigment and different kinds of micro-organisms, the latter being often present in vast numbers.

The large intestine contains in addition to the feces more or less gas, consisting at one time or another of hydrogen, carburetted and sulphuretted hydrogen, carbon dioxide, and nitrogen,which are not infrequently also eliminated by the rectum. These gases are developed, as already mentioned, during the putrefaction of proteid food, most of the nitrogen, however, being derived from the air swallowed with food.

Defecation.

In health the feces are usually discharged once in twenty-four hours. This rule, however, is far from being invariable, being modified by individual peculiarities.

Indeed, there are well authenticated cases of the act of defecation not having been performed during a period of eight years, and even longer, the unabsorbed food apparently having been either rejected by the mouth, or eliminated by the skin or kidneys. On the other hand, there seems to be no reason to doubt that there have been also cases in which the bowels were evacuated as often as twelve times daily, and that for thirty years, and yet without the health being affected.[1]

[1] Dunglison, Human Physiology, 8th ed., Vol. i., p. 191. Philadelphia, 1856. Chapman, Lectures on the Diseases of Thoracic and Abdominal Viscera, p. 294. Philadelphia, 1844.

The feces are gradually passed through the contraction of the muscular fibers of the large intestine into the sigmoid flexure of the colon, where they accumulate, and are retained for some time. It is probably the descent of the feces from the sigmoid flexure of the colon that is the immediate cause of the desire to defecate, the action being to a certain extent, as we shall see, under the control of the will. It is often thought that the feces accumulate in the rectum; the lower part of the rectum, however, in health is almost always empty, though in old persons, or in those of a constipated habits, the feces are often found there.

In the act of defecation, the feces first pass from the sigmoid flexure of the colon into the upper constricted part of the rectum, then into the lower portion, the sphincter muscle at first resisting, then giving away, through the inhibition of the nervous centers controlling the sphincter ani, and the fecal mass leaves the body. The action is assisted by the levator ani, which favors the relaxation of the external sphincter, and by the compression of the viscera through the action of the diaphragm and the abdominal muscles. When the glottis is closed a point of support is further given to the latter muscles.

Résumé of Digestion.

In concluding the subject of digestion, it does not appear to be superfluous to give a brief résumé of the different processes of which we have given a somewhat detailed account.

The food, after having been taken into the mouth, is masticated, and through the action of the tongue and cheeks having been collected into a bolus, is then swallowed. The saliva poured into the mouth acts mechanically, aiding mastication and deglutition; and chemically, in converting some of the starch into maltose, etc.

The proteid substances of the food are converted into peptones, and cane sugar to some extent into glucose, by the gastric juice, which has also the effect of dissolving the walls of the fat vesicles, the fat itself thus set free, however, being unaffected by this secretion. That part of the starch which has escaped conversion by the saliva either in the mouth or stomach, passes together with the cane sugar unchanged into the small intestine.

The intestinal juice supplements the action of the saliva upon starch, of the gastric juice upon proteids and cane sugar. The pancreatic juice converts starch into maltose, proteid into peptone, and splits the fat into fatty acid and glycerin, so rendering it susceptible of emulsion. The bile assists in the emulsifying of fats, and promotes their absorption; it further retards putrefaction, and in stimulating the peristaltic acid of the intestine acts as a natural purgative.

The conversion of starch into maltose, of albumin into peptone, etc., appears to consist in a hydration of these substances, brought about by the presence of ptyalin, pepsin, etc., entering into the

composition of the saliva, gastric juice, etc., respectively. These enzymes or ferments to which the action of the alimentary secretions is due, are elaborated out of the blood, and stored up during the intervals of digestion by the cells of which the glands consist. The ptyalin, pepsin, trypsin, etc., poured out at the moment of secretion, differ somewhat from the principles actually present in the gland during the intervals of digestion, being developed out of the latter at the moment of secretion. That the phenomenon of secretion is not one of mere filtration, is shown by the pressure exerted by the secretion, and that chemical action is going on is made evident through the heat and carbon dioxide developed.

The contents of the large intestine consist essentially of the undigested part of the food, decomposed bile, and of such digested principles as have not been absorbed. As these pass through the large intestine they gradually assume the consistence, color, odor, etc., of the feces. The latter accumulating in the sigmoid flexure of the colon, pass into the rectum and thence out of the body, their expulsion constituting the act of defecation.

CHAPTER IX.

ABSORPTION.

While the digested food in the alimentary canal may be said to be inside of the body, using the word in its ordinary acceptation, physiologically it is still outside of it, for if the food simply remained in the alimentary canal it would be of no use for nutritive purposes. Indeed, unless the digested food gets into the blood, and is so carried to all parts of the organism, and repairs the waste of its tissues, and supplies the material for the liberation of energy, it might as well not be taken into the system at all. The process by which the digested food passes from the interior of the alimentary canal into the blood, is known as absorption.

It is not to be understood, however, that absorption is by any means limited to the alimentary canal, or that the substances of which food consists are the only ones that can be absorbed. We shall soon see that oxygen is absorbed by the blood as it circulates through the lungs, that the skin will take up various substances, and that effusions found under certain circumstances in the cavities of the pleura, pericardium, peritoneum, etc., can be absorbed by these serous surfaces. Inasmuch, however, as we have just seen how the food is digested, our study of absorption will begin with the consideration of the process as it goes on in the alimentary canal.

That the ancients were well aware that the human body absorbs, is evident from their writings. Thus Hippocrates,[1] for example, speaks of "the veins of the stomach and intestine attracting the clearest and most fluid parts of the solid and liquid food."

While the ancients were correct in considering the veins as a means of absorption, it must not be inferred, however, that the course of the circulation was understood by them, it not being learned until modern times that the venous blood from the capillaries of the stomach and intestine is conveyed by the gastric and mesenteric veins to the portal vein and thence to the liver and from the latter by the hepatic vein and inferior vena cava to the heart. Nothing, however, appears to have been known in ancient times of the lymphatic system. It is well known that in the writings of Galen there are preserved vague illusions, like those of Erasistratus,[2] "to arteries in the mesentery," "full of milk," and of Hierophilus[3] to "particular veins ending in certain glands," but the context shows that these old anatomists regarded the vessels alluded

[1] Opera Omnia, p. 119. Ludg. Batav., 1665.
[2] Galenus, Opera Omnia, Tomus i., Cap. 5, p. 61. Venetiis, 1556.
[3] Ibid., Cap. 19, p. 141.

to, which were, no doubt, lymphatics, as nutrient, and not as absorbent in their function.

While it is true that the upper part of the thoracic duct in the horse was described by the Roman anatomist Eustachius[1] in 1563, the history of the lymphatic system really begins with Gasparis Aselli's discovery, in 1622, in the dissecting amphitheatre at Pavia, of the lacteals of the small intestine in the dog. Aselli tells us in his work[2] on the lacteals that, on opening a dog to show some friends the recurrent laryngeal nerves, he was surprised to find in the mesentery, in addition to the arteries and veins, delicate, white lines, which, at first, he thought were nerves. On pricking one of them, however, and seeing a whitish, milk-like fluid escape, he exclaimed, like Archimedes of old, "Eureka!" for he felt he had made a great discovery.

Aselli further extended his observations to other animals, and found the lacteals in cats, lambs, pigs, cows, and the horse. It was not, however, until 1628, two years after Aselli's death, that the lacteals were demonstrated in man. For this observation science is indebted to Peirese, Senator from Aix, who, wishing to know whether Aselli's discovery could be extended to man, permitted the body of a criminal who had been executed to be opened, when the lacteals were found (Fig. 47), the anatomist interested in the post-mortem examination having attended to the feeding of the criminal before execution.

Aselli supposed that the lacteals which he had discovered in the mesentery carried the chyle to the liver. This error was corrected by Pecquet,[3] a Frenchman, who showed, in 1649, that in the dog, and afterward in the horse, ox, pig, etc., the mesenteric lymphatics, or lacteals, terminated in a reservoir, the receptaculum chyli, now often called in honor of its discoverer the reservoir of Pecquet; and further, that this receptaculum was the beginning of the thoracic duct. The functional significance of the forgotten discovery of Eustachius became then for the first time apparent, for it was shown that the lymphatics of the small intestine and thoracic duct offered a route by which the digested food could be carried from the alimentary canal to the blood in the subclavian vein, and thence to the heart. Two years after the important discovery of the receptaculum chyli—that is, in 1651—lymphatics were demonstrated in the liver and other parts of the body by Rudbeck[4] and Bartholinus,[5] and their course and connection with each other and the mesenteric lymphatics made out.

[1] Opusc. Anat., Antig 13, p. 280. Ludg. Batav., 1707.

[2] De Lactibus Sine Lacteis Venis, Cap. ix. Mediolani, MDCXXVII.

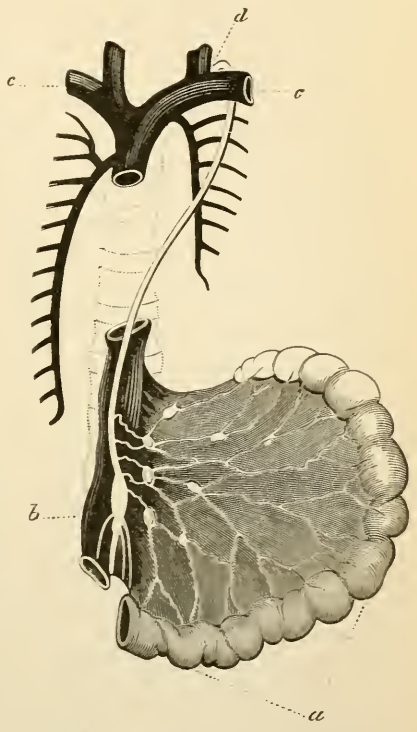
[3] Joannis Pecqueti, Diepæi Experimenta Nova Anatomica, Cap. v. and vi., Amst., 1661.

[4] Olai Rudbeck, Nova Exercitatio Anatomica exhibens ductos hepaticos aquosos vasa glandularum serosa. Clericus & Mangetus, Bibliotheca Anatomica, Tomus ii., p. 629. Genevæ, 1699.

[5] Thomæ Bartholinæ, Anatomia de Lacteis Thoracis et vases Lymphaticis. Hagæ Com, 1666.

The lymphatic system in general consists of vessels which, beginning as capillary spaces in the skin, mucous membrane, glands, etc., within the tissues, converge toward each other and gradually uniting with larger and larger trunks finally terminate in the subclavian veins as the right and left thoracic ducts. The lymph from the right side of the head and that from the upper extremity passes into the blood of the right subclavian vein, while that from the rest of the body, including the lymph and chyle from the small intestine, is conveyed into the blood of the left subclavian vein by the left thoracic duct (Fig. 47).

FIG. 47.



Lacteals, thoracic duct, etc. *a*. Intestine, *b*. Vena cava inferior. *c. c*. Right and left subclavian veins. *d*. Point of opening of thoracic duct into left subclavian. (DALTON.)

The lymphatics, in their general structure, resemble very closely the veins, consisting, like these vessels, of three coats, an external one, composed essentially of white fibrous tissue; a middle muscular elastic coat, the elastic muscular fibers being arranged circularly, and an internal epithelial layer constituting the internal coat. The lymphatics also contain valves, consisting usually of two semilunar folds.

Here and there, along the course of the lymphatics, solid bodies may be seen varying in size between a hemp seed and an almond, which apparently surround the vessels, and through which the contents must pass in their way to the thoracic ducts. These bodies are the lymphatic glands, and are more evident in certain parts of the body than in others, being well developed, for example, in the cervical, axillary, and inguinal regions. The minute structure and uses of these glands will be described when the elaboration of the blood is considered. The lymphatics not only connect the interstices of the tissues with the blood, beginning in the one and ending in the other, but they also communicate with the serous cavities. Indeed, the serous cavities, like the peritoneum, pleura, etc., can be regarded morphologically as dilated lymphatic sacs lying[1] between the viscera, these inter-

[1] The Lymphatic System, p. 222. Recklinghausen, Stricker's Histology. New York, 1872.

organic spaces representing on a large scale the minute inter-lacunar spaces, which we have just seen often constitute the beginning of a lymphatic.

Lymphatics are found very generally throughout the system. According to Sappey,[1] however, they have never been demonstrated in teeth, hair, nails, etc. Possibly, though, future researches may show that lymphatics exist even in such situations.

It is only within recent years that the fluid contained in the lymphatics, or lymph, has been satisfactorily studied. The lymph obtained by experiments made upon animals in the beginning of this century was in too small quantities to admit of thorough analysis, while the human lymph examined was probably abnormal. It was only as recently as 1853 that Colin[2] succeeded in making a fistula in the thoracic duct of the horse, and showed by this method of investigation that large quantities of normal lymph could be obtained in a short space of time.

Lymph is a transparent, yellowish, alkaline liquid; the opaline appearance that it sometimes exhibits is due to small particles of fat, while the rosy tint that is often observed in it is caused by the red corpuscles that have passed into it from the blood. When examined under the microscope, lymph is seen to consist of a liquor, and small bodies floating in it, the lymph corpuscles or globules. These measure on an average about $\frac{1}{100}$ of a mm. ($\frac{1}{2500}$ of an inch); they are homogeneous or granular in appearance, and are indistinguishable, as we shall see, from the white corpuscles of the blood. When we come to study the red blood corpuscles in man and animals, one of the most striking facts to be noted will be the great difference in their size. As regards the lymph or white corpuscles, however, it has been shown that their average diameter bears no relation to that of the red corpuscle, being as large, for example, in the musk deer, where the red corpuscle is small, as in man where it is large. Further, the white corpuscle in birds is usually smaller than that of mammals, whereas the red corpuscle of birds is larger than that of the mammal, while in the frog both the white corpuscle and the red are larger than those of the mammal.

Like the blood, the lymph coagulates when drawn from the living body. This is due in both cases to the fibrin which these fluids contain. The lymph clot, however, is less solid than that of the blood, and little or no serum exudes from it. The clot consists not only of fibrin, but of the lymph corpuscles that the lymph carries.

Chemically the liquors of the lymph differs, as we shall see, from the liquor of the blood quantitatively, rather than qualitatively, both these fluids consisting essentially of water, proteid, fibrin, and salts. Usually the lymph contains as much fibrin as the blood, but less proteid. There is more water in the lymph than in the blood, but the amount of salts in both liquids is about the same.

[1] Anatomie, tome deuxième, p. 791.
[2] Phys. Comp., 1856, Tome ii., p. 100.

From the fact of these two liquids, the liquors of the lymph and blood, being alike in their chemical composition, it has been inferred that the lymph is nothing but that part of the blood which has escaped, leaked out, so to speak, from the vascular system into the surrounding tissues, and which is afterward soaked up by the lymphatics.

COMPOSITION OF THE LYMPH.[1]

Water	95.0
Solids	5.0
Fibrin	0.1
Proteids	4.1
Fat, etc.	Traces
Extractives	0.3
Salts	0.5

While the question has not yet been definitely settled, it may be mentioned as appropriately here as elsewhere, that according to the researches of Heidenhain[2] the formation of lymph cannot be attributed to the simple filtration and diffusion of the blood plasma, some kind of secretory action being exerted by the endothelial cells of the walls of the capillaries as well. The gases of the lymph consist principally of carbon dioxide with some nitrogen and traces of oxygen.

It has already been mentioned that the red corpuscles often found in the lymph are really red blood corpuscles that have escaped from the capillaries. While it is possible that some of the lymph corpuscles may also be only white blood corpuscles that have passed from the blood with the red ones into the lymph, the lymph corpuscles in general appear to originate in an entirely different manner, there being good reasons for supposing that they are produced in the lymphatic glands, spleen, etc. The consideration of the origin of the lymph, or white corpuscles, and their relation to the red ones and the glands just mentioned, we will, however, defer until the blood is studied, and pass on to the consideration of the quantity of the lymph, and the causes of its flow through the system.

Naturally, from the conditions of the case, the amount of lymph produced can be estimated only approximately. It may be mentioned, however, that nearly six kilos (13 pounds) of lymph were collected in twenty-four hours from a lymphatic fistula in the arm of a woman by Gubler and Quevenne.[3] Various causes have been assigned for the flow of lymph. Of these, some are more important than others. One of the principal causes of the flow of the lymph is undoubtedly the *vis a tergo* resulting from the constant passing of the serum of the blood into the lymphatic system, and as the lymph, on account of the valves (Fig. 48) in the vessels, must flow always from the periphery or the radicles of the system,

[1] Landois, op. cit., p. 393. [2] Pflüger's Archiv, Band xlix., 1891, s. 209.
[3] Landois, op. cit., p. 394.

toward the great trunks and blood vessels, each successive addition of serum to the lymphatic system will act as a force propelling forward the lymph already there.

From the fact that the lymphatics contain unstriped muscular fiber, it is probable that these vessels at times contract upon their contents. This action, however, would appear to be slight, inasmuch as the rhythmical contractions of the lymphatics in mammals are rarely observed. It should be mentioned in this connection, however, that frogs, toads, lizards, etc., the lymphatics of which are unprovided with valves, possess the so-called lymphatic hearts. The latter are dilated portions of the lymphatics, exhibiting contractility, and which pulsate regularly.

Fig. 48.

Valves of the lymphatics. (Sappey.)

The influence of muscular contractions upon the flow of the lymph must not be forgotten, for pressure upon the lymphatics from this source will have the same effect as we shall see it has in accelerating the flow of blood in the veins.

From the disposition of the terminal portion of the lymphatic system in the thoracic cavity, it might naturally be inferred that during inspiration, inasmuch as all the parts are dilated, that the flow of lymph into the thoracic ducts would be increased, and that, during expiration, as all of the parts are contracted, the lymph will then flow onward into the left subclavian vein, regurgitation being impossible through the presence of valves. Experiment has shown that such is in fact the case. With each inspiration the thoracic ducts become dilated through the increased flow of lymph; at that moment the lymph flows freely from the right thoracic duct into the right subclavian vein. With each expiration the lymph is expelled with increased force from the left thoracic duct into the left subclavian vein, and when a fistula is made in that situation the lymph issues as an intermittent jet.

Of the different causes just given for the flow of the lymph, it would appear that the *vis a tergo* and the respiratory movements are the most important, the contractility of the vessels and the pressure of surrounding parts being of secondary importance.

Up to this moment, in speaking of the lymphatic system, we have only alluded incidentally to the lymphatics of the small intestine, or the lacteals. As these vessels have a special interest for us in connection with the absorption of the digested food, let us study them now a little more in detail.

The lacteals, or lymphatics of the small intestine, begin in the villi, which structures we only alluded to in speaking of the alimentary canal, reserving for the present moment their more detailed consideration. The villi (Fig. 49) are small processes of the mucous

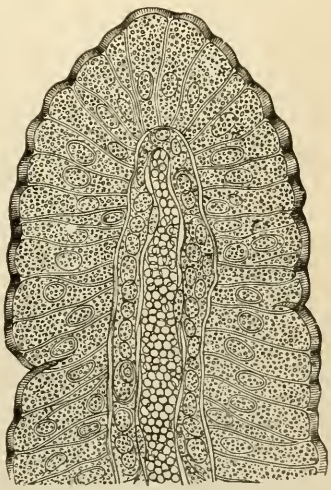
membrane of the small intestine, measuring on an average about the $\frac{1}{14}$ of a mm. ($\frac{1}{36}$ of an inch) in length, and about the $\frac{1}{28}$ of a mm. ($\frac{1}{72}$ of an inch) in breadth. They are usually conical, and flattened in form, though sometimes cylindrical, or terminating in an enlarged or clubbed-like extremity. The villi are largest and most numerous in the duodenum and the so-called jejunum. They are closely set upon the inner surface of the intestine over the valvulæ conniventes, as well as between the same, and give rise to the characteristic velvety appearance of the mucous membrane in this situation.

It has been estimated that in the upper part of the small intestine there are fifty to ninety villi to the square line, their total number amounting to about four millions. The villi can be well seen by examining a piece of intestine under water with a simple lens, the mucus having been first removed by gentle washing. When studied with the microscope the villus is seen to consist of a prolongation of the epithelial layer of the mucous membrane of the intestine, enclosing a network of blood vessels, the beginning of the lymphatics, or the lacteals, and some plain muscular fibers. These structures are held together and supported by lymphoid or retiform tissue, which,

FIG. 49.

Villus of man with lacteal and blood vessels injected. (TEICHMANN.)

FIG. 50.



Villus of man showing lacteal surrounded by epithelial cells. (FREY.)

at the surface, is condensed into a basement membrane, upon which the epithelial cells rest. (Fig. 50.)

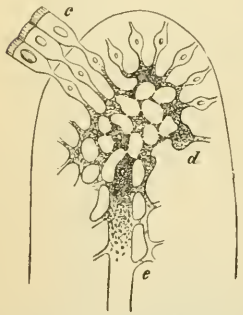
Up to this time it is doubtful if nerves have been demonstrated

in the villi. It is very probable, however, that they are present. Each villus usually receives one arterial twig, which, after penetrating it, breaks up into capillaries situated just beneath the basement membrane. The blood is returned usually by one vein. The lymphatic, or the lacteal, begins in the center of the villus, usually as a single vessel (Fig. 49), with a closed and somewhat expanded extremity. Its caliber is considerably larger than that of the capillary blood vessels surrounding it.

The lacteal within the villus, like the lymphatics elsewhere, is surrounded by a delicate layer of flattened epitheloid cells (Fig. 50). These are connected with the cells of the basement membrane through those of the lymphoid or connective tissue lying between (Fig. 51).

The columnar epithelial cells which cover the villi, and also the surface of the mucous membrane, and which are prolonged into the tubular glands, present a granular appearance with an oval nucleus. They terminate toward the basement membrane in a tapering manner, and measure about the $\frac{1}{40}$th of a mm. ($\frac{1}{1000}$ of an inch) in length. Their free end (Fig. 51), or the surface looking toward the interior of the intestine, consists of a layer of a highly refractive substance, with vertical striæ running through it. These striæ have been regarded as being either minute canals, or as solid rods. Some of these columnar cells usually contain mucus, and swell up upon the addition of water into the so-called goblet cells which are regarded by some anatomists as the true beginning of the absorbent system.

Fig. 51.



Diagrammatic representation of the origin of the lacteals in a villus. *e*. Central lacteal. *d*. Lymph channels. *c*. Columnar epithelial cells, the attached extremities of which are directly continuous with the lymph channels.

The lymphatic or central lacteal connected with the columnar cells by the lymph channels in the stroma after emerging from the villus passes into the lymphatics of the intestine. These are usually described as consisting of two sets, the deep and superficial. The latter pass into the mesentery to the lymphatic glands. The lymphatics coming from the latter, as we have seen, converge toward the receptaculum chyli.

During the intervals of digestion the lymphatics of the small intestine, or the lacteals, contain lymph, undistinguishable from that of the lymphatics of the rest of the body. During digestion and absorption, however, and more especially when fatty articles have constituted part of the food, the epithelial cells of the villi, and the lymphatics of the small intestine, are then filled with the chyle. The chyle is a coagulable, alkaline, opaque, whitish, milky-like fluid, hence the name of the lacteals given to the lymphatics of the small intestine, in which it is found.

COMPOSITION OF THE CHYLE.[1]

Water	90.5
Solids	9.5
Fibrin	0.1
Proteids	7.0
Fat, etc.	1.0
Extractives, Salts	1.4

The chyle, however, is only the lymph with the products of digestion added to it, and as the lacteals absorb principally the fat, the essential difference between the chyle and the lymph is that the former contains a great quantity of fat, the latter usually only a trace. In reference to any analysis of the chyle, it must not be forgotten that its composition will differ according to whether the portion examined has been taken from the lacteals or the thoracic duct. Indeed, chyle drawn from the thoracic duct is not pure chyle, but chyle mixed with the lymph which has been brought from the extremities to the receptaculum chyli, and thence passed into the thoracic duct.

The chyle of the thoracic duct will contain, therefore, less fat and other solid constituents, than that of the lacteals. Further, the amount of fat in the chyle will be variable, depending upon the diet of the man or animal examined. Thus, the chyle of a carnivorous animal will contain more fat than that of a herbivorous one, the food of the former being richer in fat than that of the latter. At one time it was supposed that the lacteals absorbed exclusively the fatty substances, but it is now known that they also take up, at least in small quantities, albuminoid and saccharine substances, salts and water.

Of the amount of the chyle poured into the thoracic duct, it is impossible to give even an approximate estimate.

When examined microscopically, the milky appearance of the chyle is seen to be due to an immense number of very minute fatty granules, which constitute the so-called molecular base of the chyle, and which measure on an average the $\frac{1}{480}$ of a mm. ($\frac{1}{12000}$ of an inch) in diameter. These granules appear to be coated with albumin, which probably prevents their running together and coalescing. The so-called chyle corpuscles found in greater or less number in the chyle, do not differ from those of the lymph or blood, and will be considered again when the latter fluid is studied.

What has been already stated in reference to the supposed causes of the flow of the lymph will apply equally well to that of the chyle; but there is one condition, in addition to those already mentioned, which appears to influence favorably the flow of the chyle, and so deserves a passing notice. It will be remembered that, in speaking of the structure of the villi, allusion was made to the plain muscular fiber that they contain. These muscular fibers are dispersed longitudinally around the lacteal, and their contraction will

[1] Landois, op. cit., p. 392.

obviously retract the villus. The effect of the action of these muscular fibers will then be to force the contents of the lacteal out of the villus into the superficial lymphatics. These muscular fibers have probably, then, some importance in aiding the flow of the chyle toward the thoracic duct.

It will be remembered that, up to the time that the lymphatics were discovered, absorption was considered to be effected by the veins only. After the discovery of the lymphatics, however, physiologists fell into the opposite error of attributing absorption solely to the lymphatics, denying that the veins took any share in this process. Indeed, it was not until the present century that it was experimentally demonstrated that the veins as well as the lymphatics absorb. Apart, however, from any experimental evidence, the facts of comparative anatomy alone should have shown that of the two sets of vessels, so far as the absorption of the digested food is concerned, the veins play a more important part than the lymphatics.

Thus it is well known that in the amphioxus, the lowest of the vertebrata, and in all the invertebrata, the lymphatic system is absent. In these animals, therefore, absorption is carried on solely by veins. Further, while the lymphatic system is present in fishes, batrachia, reptiles, and birds, it is only in the mammalia that it acquires the functional importance that we have ascribed to it.

Indeed, according to Bernard,[1] the name lacteal cannot be properly applied to the lymphatics of the small intestine in the oviparous vertebrates, since these lymphatics contain always, even during digestion, with few exceptions, a clear, transparent lymph instead of chyle, an opaque, whitish fluid, the fat in these animals being taken up, not by the so-called lacteals, but by the portal vein, the greater part of it being thence carried to the renal veins (Jacobsen's system), and so to the vena cava.

Inasmuch as absorption is carried on by the veins in the lower animals, we would naturally infer that these vessels must be of great importance in this respect in man and the mammalia. Magendie[2] appears to have been the first to show conclusively by experiment that absorption takes place by the blood vessels.

Of his many remarkable and accurate experiments, the following may be mentioned: In one experiment the abdomen of a dog that had been well fed some hours previously was opened, and a loop of the intestine drawn out. Ligatures were placed around this loop at a distance of about 37.5 centimeters (15 inches) apart. The lymphatics arising from this portion of the intestine being all ligated in two places, were divided between the ligatures. Of the five mesenteric arteries and veins passing into the general vascular system, four were divided and ligated so that the loop of the intestine remained in connection with the rest of the system by only a single vein and artery, even the cellular coat of which was dissected off,

[1] Physiologie Experimentale, Tome ii., p. 312.
[2] Journal de Physiologie, p. 18. Paris, 1821.

so as to remove all doubt of there being a trace of a lymphatic left. Some upas was then introduced into the loop of the intestine prepared in the above manner, which was then replaced in the abdomen, and in a few minutes the characteristic symptoms of poisoning appeared, showing that the upas had been absorbed by the vein.

In another experiment, where the poison was introduced into the foot, the only connection between the limb and the rest of the body was through two quills, introduced into the divided femoral blood vessels, the rest of the parts having been dissected off. In this case, also, the only possible means by which the poison could pass into the general system and make its effects evident was through the circulating blood.

The experiments of Magendie were soon afterward confirmed by Tiedmann and Gmelin,[1] Segalas,[2] and by the committee appointed by the Academy of Medicine of Philadelphia to investigate the subject.[3]

A convenient method of demonstrating venous absorption is to open the abdomen of a frog, withdraw a loop of the intestine, and ligate it in two places, cut away all the mesentery, leaving only a single artery and vein, and introduce a solution of ferrocyanide of potassium into the intestine by an opening made in the latter, replace the loop within the abdomen, and, after a few minutes, open one of the veins of the foot. On testing the blood for the ferrocyanide of potassium by adding tincture of the chloride of iron, the presence of the salt introduced into the intestine will become at once evident, through the formation of Prussian blue, the latter being best demonstrated by adding the perchloride of iron to the serum, the blood having been allowed to stand, or to a clear extract of the blood, made by boiling the latter with a little sodium sulphate and filtering.

It is obvious that the only means by which the salt of potassium could pass under such circumstances from the intestine into the general circulation, and thence into the blood of the extremities, was by means of the vein left in the mesentery.

As we have seen that by far the greatest part of the food is digested in the small intestine, it might be naturally inferred that the water, salts, peptones, sugars, and fat are absorbed by the veins and lymphatics of the small intestine rather than by those of the stomach. That such is the case appears to have been shown, at least in animals. Thus, for example, in a dog, in whom a fistula of the duodenum had been established, of the water drunk fully 99 per cent. passed within twenty minutes out of the fistula.[4]

[1] Recherches sur la route qui prennent diverses substances pour passer d' Estomac et du Canal intestinal dans le Sang. Paris, 1821.

[2] Journal de Physiologie, Tome ii., p. 117. Paris, 1822.

[3] Philadelphia Journal of the Med. and Phys. Sciences, 1821, Vol. iii., p. 273; 1822, Vol. v., p. 327.

[4] J. Von Mering, Therapeutische Monatshefte, Berlin, 1893, s. 201. J. S. Edkins, Journal of Physiology, 1892, Vol. xiii., p. 445. Brandl, Zeits. für Biologie, 1892, Band 29, s. 277.

Salts do not appear to be absorbed by the stomach unless introduced into the latter in a more concentrated state (3 per cent.) than when taken as food. Sugars and peptones appear, however, to be absorbed by the stomach to some extent, especially if the solutions are concentrated (5 per cent.). The absorption of salts, sugars, and peptones by the stomach is much increased if given with alcohol and condiments, such as pepper and mustard. Alcohol itself is readily absorbed by the stomach.

As fat to be absorbed must first be emulsified and as that change is only effected in the small intestine, it is evident that fat must pass through the stomach without being absorbed. Apart from the fact that food is rendered fit for absorption largely by digestion in the small intestine, it should be mentioned that ample time is afforded for its absorption by this part of the alimentary canal, since from nine to twenty-three hours elapse before the food eaten passes out of the small into the large intestine, its passage being retarded by the presence of the villi and valvulæ conniventes. Experiments made upon animals,[1] and observations upon human beings,[2] confirm the view based upon the above considerations, that water, salts, peptones, sugar, and fat are principally absorbed by the small intestine. In considering the water and salts absorbed by the veins of the small intestine, it must be borne in mind, however, that as part of the water, etc., absorbed is replaced by that excreted by the intestine, the contents of the latter are, therefore, more or less liquid like the chyme. As a proof of the amount of proteid absorbed, it may be mentioned that in a case of fistula of the end of the ileum in a human being, about eighty-five per cent. of the proteid eaten was absorbed before the latter reached the large intestine. It should be mentioned, in this connection, that while peptones and albumoses are without doubt absorbed by the veins of the stomach and small intestine, they are not found as such in the blood. The only conclusion to be drawn from this fact is that peptones, etc., are converted into serum or blood albumin as they pass through the epithelial cells into the blood. If such be the case then peptones, etc., must, in becoming blood albumin, undergo in the epithelium dehydration and polymerization, the reverse of the processes by which they were produced from proteid, viz., hydration and splitting. The various carbohydrates appear to be absorbed by the veins of the small intestine in the form of glucose, or glucose and levulose. Thus, starch is converted into maltose and then into glucose, cane sugar into glucose and levulose, lactose into glucose and galactose; lactose appears, however, under certain circumstances to be absorbed as such unchanged. While the water, salts, sugar, and peptones are usually absorbed by the veins, the emulsified fat is taken up by the lymphatics of the small intestine or the lacteals.

[1] Macfadyen, Nencki, u. Sieber, Archiv für exper. Path. u. Phar., Band 28, 1891, s. 311.

[2] Röhmann, Pflüger's Archiv, 1877, Band 41, s. 411.

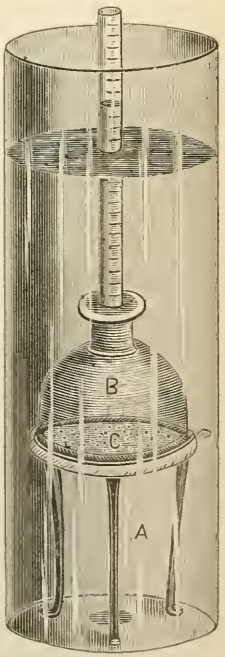
Recalling what has just been said of the structure of a villus, it will be seen that the lymph channels in the stroma afford a pathway by which the fat taken up by the cells will be carried into the central lacteal. There appears to be no doubt that the water, salts, peptones, sugar, that escape absorption in the small intestine are taken up by the veins of the large intestine, ample time being afforded since the time required for the passage of the food residue through this portion of the alimentary canal amounts to about twelve hours.

We have seen that the principal function of the lymphatics of the small intestine is to absorb fat, nevertheless they can and do take up peptones, glucose, and water; on the other hand, the mesenteric veins, in addition to absorbing these latter substances, may take up also, at times, considerable quantities of fat. Briefly, then, the functions of the lymphatic and venous absorbents are essentially the same; as a rule, however, the fats pass into the blood by the one route, the remaining alimentary substances by the other.

Osmosis.

We have seen that during absorption the digested food passes from the interior of the alimentary canal into the veins and lymphatics. The investigation of the causes of the phenomena of absorption resolves itself, therefore, into the determination of the conditions on which depend the passage of peptone, glucose, etc., and emulsified fat through the epithelium of the alimentary canal and the wall of the capillary or lymphatic into the blood or lymph.

Fig. 52.



Graham's osmometer.

In physical science the diffusion of liquids into each other when separated by a membrane is known as osmosis. Let us consider, briefly, what is understood by the term osmosis, and see to what extent the facts of absorption that we have described can be explained by this principle.

A convenient method of illustrating the phenomena of osmosis is to close one end of a bulbous glass tube (Fig. 52) B with a membrane-like parchment C, and having placed within the tube a solution of some salt, potassium bichromate, for example, to immerse the tube or the osmometer, as it is called, in a vase of distilled water A. In a few moments the potassium salt will pass through the membrane into the water of the vase (exosmosis) imparting to the latter a yellowish hue, and the water of the vase, through the membrane, into the salt solution in the tube (endosmosis), the level of the solution in the tube

rising, that in the vase falling. After a certain length of time has elapsed, varying with the substances used, strength of solution, and other conditions, the passage of the salt into the water in the one direction and of the water into the salt solution in the other ceases. It will then be found that the proportion of the salt in the water of the vase and in the water of the tube is the same, but that the volume of water in the tube has been greatly increased. The ratio of the weight of the water of the vase passing into the solution of the tube to that of the salt passing into the water of the vase is called the "endosmotic equivalent," and is usually expressed thus $\frac{\text{Water}}{\text{Salt}}$. It should be mentioned, however, that this ratio is not a constant one, varying with the strength of the solutions used. A more delicate way of illustrating osmosis is to replace the jar of the last experiment with an egg prepared in the following way: At one end of the egg the shell is removed in such a way as to leave the lining membrane of the egg intact; at the other end, shell and membrane are both perforated sufficiently to permit the passing of a glass tube into the egg; which is held securely to the egg by sealing wax. The egg is then passed in a wine glass of water, and the level of the water noted. Shortly afterward the yellow of the egg will be seen rising in the tube, and the level of the water falling in the wine glass. The water of the glass gradually passes through the membrane of the egg, distending it, and forcing the contents of the egg upward. On the other hand, the salts of the egg—the chlorides, phosphates, sulphates—will be found to have diffused away from the rest of the egg into the water of the glass, as can be readily shown by appropriate tests. Thus, if a few drops of silver nitrate be added to the water, at once silver chloride will be formed and precipitated, showing that the sodium chloride has passed into the water.

An important fact to be noted, the physiological significance of which will be appreciated shortly, is that little or no albumin is found in the water, scarcely a trace of it, if any, passing through the egg membrane, particularly if the water be distilled. In this experiment also, as well as in the preceding one, the substances on either side of the membrane (in the case of the egg, most of them at least) diffused into each other. This, as we shall see in a moment, depends not only on the membrane being capable of imbibing both liquids, but also that the latter were miscible with each other. If a membranous septum, however, be used, which will imbibe only one of the liquids, that one alone will traverse the septum, will increase the volume of the other liquid if it is miscible with it, but there will be no exchange of liquids.

The name of Dutrochet[1] is invariably associated with any discussion of the phenomena of osmosis. The history of the subject

[1] Memoire pour servir a la Histoire Anatomique et Physiologiques des Animaux. Paris, 1837, Tome 1.

teaches us, however, that the discovery of this important physical principle, like that of all others, was not a sudden, but a gradual one. Many of the phenomena had been observed, and numerous experiments bearing upon the subject had been performed and recorded before the time of the distinguished French physiologist. The merit of Dutrochet consisted in not only devising and performing new experiments, but of generalizing the facts of osmosis, and applying them to the explanation of absorption in living beings.

This able investigator described thoroughly the passage of liquids through animal membranes; he showed the influence of different liquids used, measured the force of the currents, constructed the osmometer, and called particular attention to the currents, naming them endosmotic and exosmotic, according as they passed into the tube from the surrounding liquid, or in the reverse direction, and applied the facts to the explanation of physiological phenomena. Since then the subject of osmosis has been most thoroughly investigated by Graham.[1] This physicist discards the terms endosmosis and exosmosis, considering that there is but one current, the inward one, and designating it by the term osmotic, and the whole phenomena as osmosis.

According to Graham, the molecules of the salt in the outward current travel by diffusion through the porous membrane. "It is not the whole saline liquid which moves outward, but merely the molecules of salt, their water of solution being passed, the inward current of water, on the other hand, appearing to be a true, sensible stream." According to this view, the only true current in the osmometer (Fig. 52) is that of the water from the jar (A) through the membrane (C) into the bulbous tube (B) containing a solution of potassium bichromate, the apparent outward movement from the jar (B) into the water in A, being due to the diffusion of the molecules of the salt. So far, however, as the physiologist is concerned, the important fact in this experiment is, that there is an exchange going on, the water passing one way, the salt the other.

Having given several illustrations of osmosis, let us consider now the causes of the same. The phenomenon of osmosis depends essentially upon two conditions: first, that the membranous septum is capable of imbibing the liquids which it separates; second, that the liquids are miscible. It will be remembered that in speaking of the organic proximate principles, allusion was made, among their other properties, to that of their taking or giving up of water. The swelling up of a tendon or muscle when immersed in water is a common example of the imbibition by organic tissues of liquids. Every organic tissue and, indeed, all substances, however solid they may appear, are more or less porous, at least in the sense that the particles of which a body consist are separated to a greater or less extent from each other. It is due to the presence of the interspaces, between the particles of which a tissue consists, that imbibi-

[1] Osmotic Force, Phil. Trans., 1854, p. 178.

tion is possible, that the tissue is capable of taking up a liquid, retaining it for some time, and finally giving it up again.

The passage of a liquid into the interspaces or interstices of a tissue is, however, an example of capillarity, the particles of which the tissue consists bearing to the liquid passing through the spaces between them the same relation that the walls of a capillary tube bear to the liquid moving within them. The ascent of the oil in the wick of a lamp is a familiar example of capillary action.

In order that an osmosis should take place, it is evident that the membranous septum must be not only capable of imbibing the liquids through capillary action, but, further, that the liquids separated by the septum must be miscible, otherwise, though the liquids might get into the septum, they would not diffuse into one another, and there would be no current. This brings us, therefore, to the consideration of the second condition of osmosis, the diffusion of liquids.

It is a familiar fact that, if a drop of water rolling over a surface, upon which it can preserve its globular form, comes in contact with a drop of mercury, or of oil, the drops do not run into each other or fuse, the particles of the drop of water having a greater affinity for each other than for the particles of the drop of mercury or of oil, and *vice versa*. On the other hand, if the drop of water meets with a drop of alcohol, the two do run into each other, losing their identity, the particles of the water having a greater affinity for those of the alcohol than they have for each other. A simple illustration of the diffusion of liquids is to place in a small vial a solution of copper sulphate and immerse the vial containing the solution in a vase of water. Soon the surrounding water will assume a blue color through the diffusion into water of the copper.

The dissolving of a substance in a menstruum is an illustration of the same principle, the molecules of the dissolving liquid having a greater affinity for the particles of the substance to be dissolved than these have for each other. The solution of a substance, however, depends not only upon the affinities, chemical or physical, existing between the particles of the substance and those of its menstruum, but also upon the fact that when the cohesive force holding together these particles ceases to act the particles become separated, repel each other, they acting then like the particles of a gas. The diffusion of liquids depends, therefore, upon the affinities existing between the particles of which the liquids consist and a repelling force of the same.

Many interesting and important facts in reference to the diffusion of liquids have been established, more particularly by the researches of Graham. It is not essential, however, that we should dwell upon these, merely indicating that the diffusibility of liquids differs very much, according to their density, composition, the character of the septum, temperature, etc.

On account, however, of its important application to physiology

it is necessary, before leaving the subject of diffusion, to call attention to the distinction made by Graham between what this physicist calls crystalloids and colloids, and which can be well illustrated by the following simple experiment: If a piece of potassium bichromate, or a little of the same substance in powder, be placed in the center of a mass of boiled starch, in a few hours the whole of the starch will be seen colored, the potash having diffused through it. On the other hand, if a piece of caramel be similarly placed on a mass of boiled starch, it will remain where placed, not diffusing at all. Substances which diffuse readily, like the salts of potassium, are termed crystalloids, while those that do not do so are called colloids. Thus, in the experiment with the egg, the sodium chloride, being a crystalloid, diffuses through the egg membrane, while the albumin, being a colloid, remains within the egg. The method of dialysis of Graham, so useful as an instrument of analysis, is based upon this distinction of crystalloids: thus, if a fluid, consisting of a mixture of organic matter and arsenic, be placed in an osmometer, in the course of twenty-four hours, perhaps, three-fourths of the arsenic will diffuse through the membrane into the surrounding water, the organic matters remaining within the jar. The application of the facts of capillarity and diffusion in the explanation of osmosis, as illustrated by the above experiments, is so evident, that it may appear superfluous to dwell further upon the subject. We will, therefore, merely call attention to the most important conditions.

In all the experiments which have just been described it is perfectly clear that the first condition of osmosis is that the liquid shall wet the membrane, or, in other words, that the membrane is capable of imbibition. This, we have seen, is due to capillary force. The second condition is, that the liquids having been imbibed by the membrane are miscible, or will diffuse, otherwise they would get no further than the interstices of the membrane, and there would be no currents. The modifications of the phenomena, according to whether the septum is solid, liquid, or semi-solid, as to whether the current is endosmotic or exosmotic, of the relative force of the two, etc., can be shown to depend upon these two conditions.

Having gone over this preliminary ground, let us now see whether the established facts of capillarity and diffusion, and the theory of osmosis deduced from them, can be applied to the explanation of absorption, as it takes place in the living body.

During absorption from the alimentary canal we have seen the digested food in a liquid or semi-liquid state passes through the epithelium, and the wall of a capillary or lymphatic into the blood or lymph. The epithelium and capillary wall in the living body are comparable, therefore, to the septum of the osmometer, the liquids in the intestinal canal and the blood and lymph corresponding to the fluids separated by the septum in that instrument.

The action of a hydragogue cathartic, such as magnesium sul-

phate, is also an illustration of osmosis, since the salt passes from the interior of the alimentary canal through the epithelial layer of the intestine and wall of the capillary into the blood, and the watery part of the blood, together with some albumin (the latter effect being due, probably, to the presence of the saline), passes into the interior of the alimentary canal. The osmosis can be experimentally imitated by placing the solution of the magnesium sulphate within the jar of the osmometer and the serum of the blood within the bulbous tube, the serum passing through the membrane into the magnesium sulphate, and the latter passing into the serum and increasing its volume.

Supposing that the jar represents the alimentary canal, and the bulbous tube the blood vessel, the osmosis going on in the experiment is essentially the same as that in the living body after the administration of a hydragogue cathartic.

The essential difference between the osmosis that takes place during absorption and after the administration of a saline and in an osmometer is that the conditions which favor osmosis are realized in a way and to an extent in the living body that cannot be imitated for a moment, even in the most delicate experiments. Thus, it has been found that the activity of osmotic currents is in proportion to the extent and thinness of the membrane. When we come to study the capillary system we shall see that the extent of absorbing surface exposed by it is enormous, and that the walls of the capillaries are extremely delicate, measuring, on an average, perhaps from the $\frac{1}{1000}$ to the $\frac{1}{480}$ of a millimeter ($\frac{1}{25000}$ to the $\frac{1}{12000}$ of an inch) in diameter.

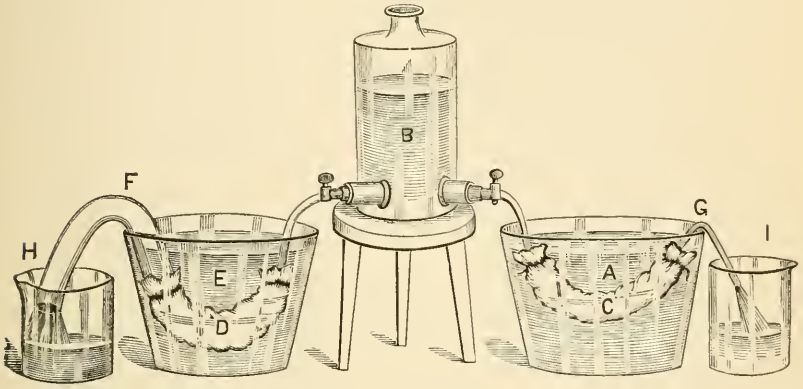
One can readily imagine how favorable such a thin septum would be in the production of osmosis. It can be shown, also, as might have been supposed, that an osmotic current is favored by having little or no pressure to overcome, such a current ceasing and beginning again, according as dense substances, like mercury, are added to or taken away from the fluid within the tube of the osmometer. Now in the living body the pressure of the blood, even in the largest arteries, seldom exceeds 150 millimeters (6 inches) of mercury, and this pressure is very much reduced as the blood flows into the capillary and venous system, so that a current flowing from the intestine toward the blood meets with no very great resistance.

An important, though not indispensable, condition favoring the osmotic current is the density of the solution in the bulbous tube of the osmometer, the flow being usually greater according to the density of the solution. Hence the activity of absorption after the administration of hydragogue cathartics, such drugs diminishing the watery constituents of the blood, and so increasing its density, while, at the same time, they diminish pressure. Again, osmotic currents are more active if the liquids are kept in movement. Thus, when osmosis has ceased, it can often be made to commence again by simply stirring the liquids. It is evident from this how great

and favorable are the influences exerted by the circulation of the blood and lymph in promoting osmosis and absorption.

The importance of the movement of the liquids, or of one of them, in favoring osmosis is shown by the simple apparatus represented in Fig. 53. A jar (B), furnished with two stopcocks, is

FIG. 53.



filled with a colored fluid, litmus water, for example. To both stopcocks are fitted equal portions of intestine (D and C), which are immersed in the vases of water E and A. Into the piece of intestine C is fitted a siphon (G) of smaller diameter than that of the intestine, a siphon (F) of as large diameter as that of the intestine being inserted into the piece of intestine D. Both siphons (F and G) pass into the vases H and I. The stopcocks of the reservoir (B) being opened, the colored fluid will flow into the two pieces of intestine, but inasmuch as the small size of the siphon G will offer an obstacle to the flow of the colored liquid through it into the vase I, the piece of the intestine C will become distended, and there will be an exosmosis from it of the colored fluid into the water of the vase A. On the other hand, the colored fluid passing readily through the siphon F, on account of its large size, the piece of intestine D will become flaccid, and there will be a rapid flow of the water of the vase E, through the intestine D, into the colored fluid flowing through it, or an endosmosis.

Too much importance must not be attached, however, to osmosis as accounting for the phenomena of absorption, as, under certain circumstances, substances are absorbed not in accordance with, but independently of this physical principle. Thus, for example, in a solution containing equal quantities of glucose and sodium sulphate, after a given time the sugar will be completely absorbed, whereas the sodium sulphate, although far more diffusible, will still remain in considerable amounts in the intestine. Again, certain coloring matters are not absorbed, the cells appearing to exert some discrimi-

nating power between different substances. The absorption of the emulsified fats is also difficult to explain by osmosis. Many other illustrations might be offered to show that while absorption appears to be due to osmosis in some instances, in others it can not be accounted for by that principle alone. Indeed to such an extent is this the case that, according to many physiologists, absorption is due not to osmosis, but to some specific action of the protoplasm of the living cell as yet not understood.

CHAPTER X.

THE BLOOD.

From time immemorial the blood has been recognized as the most important fluid in the human body, as well as in that of animals—indeed, as indispensable to life. Daily observation continually shows that its loss prostrates the body and enfeebles its powers, and, with excessive hemorrhage, that life itself ebbs away.

This is readily understood when it is known that the blood in circulating through the economy carries to the tissues, and the cells composing them, material for their growth, renewal, and repair, and removes from them that which has become effete and worn out and equalizes more or less the temperature throughout the body. The blood is an alkaline fluid, due to the alkaline salts, especially sodium carbonate, dissolved in the plasma. The degree of alkalinity, estimated as Na_2CO_3, corresponds in human blood to 0.35 per cent. of this salt. The specific gravity of the blood when defibrinated amounts upon the average to from 1.055 to 1.063. Recent researches[1] have shown, however, that the specific gravity varies in individuals, with age and sex, with eating and exercise, the hour of the day, etc.

The opacity of the blood is due to the fact that it is not a homogeneous liquid, being composed, as we shall see presently, of two elements—corpuscles and liquor sanguinis, or plasma; these, differing in their refractive power, offer an obstacle to the transmission of light, which is lost in its passage from the air through the liquor and corpuscles. The blood has a saltish taste, and a faint but distinct odor. This becomes more apparent when a few drops of sulphuric acid are added to the specimen examined. It may be mentioned, in this connection, that the importance of the odor of the blood, as made use of in criminal cases, and often insisted upon by medico-legal writers, has been grossly exaggerated.

The temperature of the blood in man, as we shall see hereafter, is on the average 37.°2 C. (98.°9 F.), but it is very probable that, in certain parts of the body, it is several degrees higher. Bernard found that in dogs and sheep the temperature in the aorta ranged from 37° C. to 40° C. (99° F. to 105° F.), and reached even 42° C. (107° F.) in the hepatic vein. According to the same authority, the blood is hotter in the right than in the left side of the heart; the temperature is higher in the arteries than in the veins, with the exception, however, of the blood in the portal vein, which is warmer than that in the aorta independently of digestion.[2] The sudden rise

[1] L. E. Jones, Journal of Physiology, Vol. viii., 1887, p. 1; Vol. xii., 1891, p. 229.
[2] Sur les Liquides des l'Organisme, Tome i., 3d, 4th, 5th lecons.

of temperature often observed in man just before death, due, perhaps, to the loss of vascular tonicity, would seem to show that the temperature of the blood in the deeper vessels in man is as high as that observed by Bernard in the animal just mentioned.

One of the most striking features of the blood is its color, red or scarlet in the arteries, blue or black in the veins. As first demonstrated by Lower,[1] this difference is due to the venous blood absorbing air as it passes through the lungs. When we come to study the circulation and respiration, we shall see that, as the red blood passes through the capillaries it loses oxygen and gains carbon dioxide, becoming blue, while it turns again into red blood in the lungs with the fresh absorption of oxygen. The blood of the pulmonary artery, however, is blue, while that of the pulmonary vein is red. The blood in the veins coming from glands, during secretion, as shown by Bernard,[2] is also red, and this is the case also in the veins when the sympathetic is cut. The explanation in these cases seems to be that the increased supply of arterial blood to the parts carries an excess of oxygen to the veins sufficient to maintain the red color of the blood flowing into them.

The brightness in color of the blood depends, to a certain extent, upon the form of the corpuscles; it is bright when they are flattened and hollowed, containing oxygen, and dark when they are distended and round, containing carbon dioxide, the reflection of the light depending on the form of the corpuscles.

Numerous experiments have been made from time to time to determine, if possible, the quantity of blood in the human body. Among others may be mentioned the often quoted ones of Weber and Lehmann.[3] These experiments were made upon two criminals who were first weighed and then decapitated. The blood remaining in the vessels after decapitation was calculated by injecting water into the vessels of the head and trunk until that which passed out by the veins exhibited only a pale yellowish color. This was evaporated, and the dry residue was assumed to represent a certain quantity of blood, the ratio of blood to its residue having been previously ascertained. The amount of blood lost by decapitation was a little over twelve pounds, and that estimated by the above method as remaining in the vessels as a little over four pounds, making for the whole body 16.59 pounds.

AMOUNT OF BLOOD IN THE BODY.

12 lbs. of blood lost in execution.
4 lbs. of blood collected by washing.
16 lbs. of blood in criminal weighing 128 lbs., or
1 lb. of blood to 8 of body weight.

[1] Tractatus de Corde item de Motu etc., Colore Sanguinis, etc., p. 180. Amstelodami, 1669.
[2] Op. cit., pp. 268, 299.
[3] Lehrbuch der Phys. Chemie, 1852, Tome ii., s. 234.

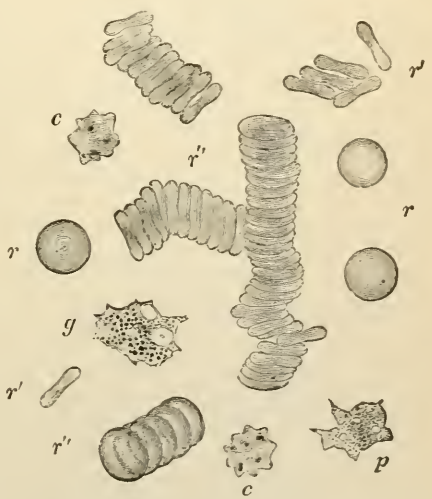
The weight of one of the criminals was 132.7 pounds; this would give a ratio of about one pound of blood to every eight of body, a somewhat higher ratio than that obtained by experiments upon dogs, the blood amounting usually in that animal to one-thirteenth of the body weight.

It must be remembered, however, that this is only an approximation, for the amount of blood left in the body after decapitation cannot be accurately determined by the method just mentioned. Further, the amount of blood in the body is notably increased during digestion. Bernard [1] has shown that an animal like the rabbit, for example, during digestion can lose twice as much blood as when fasting. Burdach [2] refers to a case reported by Wrisberg of a woman losing over twenty-one pounds of blood after decapitation. Facts like these show the importance of taking into consideration the state of the system in determining the quantity of blood. In a general way this may be stated in an adult healthy man to amount to sixteen or twenty pounds and is distributed, according to Ranke,[3] in round numbers as follows:

¼ vascular system.	¼ skeletal muscles.
¼ liver.	¼ remaining organs.

When the blood is examined under the microscope, for example, circulating in the web of a living frog's foot, it will be seen to consist, as already mentioned, of two distinct portions, a transparent colorless liquid, the liquor sanguinis or plasma, and of minute bodies or corpuscles, the blood globules or blood cells. The corpuscles which float in the liquid part of the blood are of three kinds, the red, the white or leucocytes, and the blood plates. The red corpuscles, discovered by Leuwenhoek [4] in 1673, are far more numerous than the leucocytes or blood plates and give to the blood its red color, they being carriers of oxygen. The yellow tint exhibited by blood plasma free of corpuscles when viewed in quantity appears to be due to the presence of a pigment the nature of which is not understood.

FIG. 54.



Human blood as seen on the warm stage. Magnified about 1200 diameters. *c*, *c*. Crenate red corpuscles. *p*. A finely granular. *g*. A coarsely granular pale corpuscle. Both exhibit two or three vacuoles. In *g* a nucleus also is visible. (QUAIN.)

[1] Op. cit., Tome i., p. 419.
[2] Traité de Physiologie, traduit par Jourdain, Tome vi., p. 116. Paris, 1837.
[3] Physiologie, 1871, s. 373. [4] Philos. Transactions, p. 23. London, 1674.

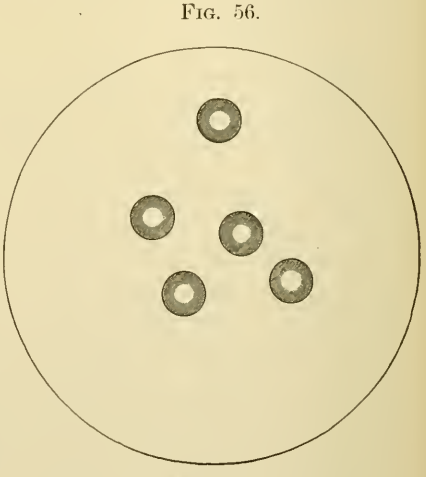
Let us study the corpuscles, first reserving for the present the consideration of the plasma or the liquor of the blood.

When blood is examined under the microscope the corpuscles will be observed in different positions, some on their edges or sides, others lying flat (Fig. 54). It can be seen that they are circular, flattened disks, about four times as broad as thick and biconcave in form. From this latter circumstance they are thinnest in the center. Therefore, when a corpuscle is viewed under the microscope from the flat side, if the edges are in focus the center will appear dark, simulating a nucleus (Fig. 55); whereas, when the center is in focus and is light the edges will appear dark (Fig. 56). In reality, however, there is neither a nucleus nor a membranous cell-wall, the red corpuscle being a homogeneous structureless mass of living matter, soft, transparent, elastic, and of a pale amber color. The red color of the blood is due to the immense number of the corpuscles. Vierordt[1] estimates that a cubic millimeter in the male contains 5,000,000, in the female 4,500,000.

Fig. 55.

Red globules of the blood, seen a little beyond the focus of the microscope. (Dalton.)

Fig. 56.



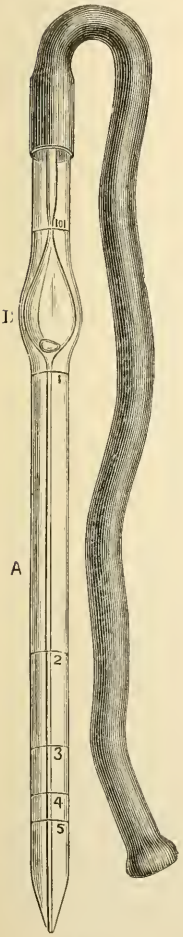
The same, seen a little within the focus. (Dalton.)

The method we make use of in counting the blood corpuscles is essentially that of Malassez and Potain[2] and Gowers.[3] It consists in sucking up into a graduated tube (Fig. 57, A) one cubic millimeter of blood and then a five per cent. solution of sodium chloride from a jar into the tube until the blood and the solution are drawn into and fill the dilated portion (Fig. 57, B) of the tube. This dilated portion having a capacity of 100 millimeters, the blood will then be diluted 100 times. One millimeter of this mixture will, therefore, contain the $\frac{1}{100}$ part of a millimeter

[1] Physiologie, s. 9. Tübingen, 1871.
[2] Archiv de Physiologie, p. 32. Paris, 1876.
[3] Lancet, 1877, p. 797.

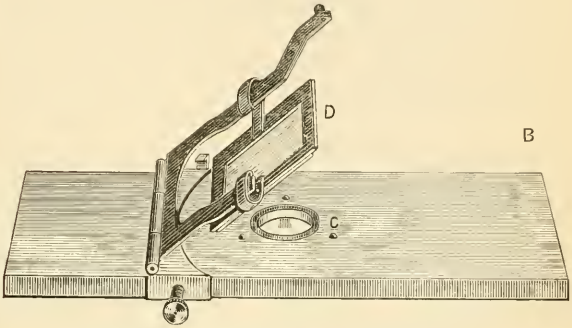
of blood and the $\frac{1}{100}$ of a millimeter of the mixture, $\frac{1}{100}$ of $\frac{1}{100}$ or the $\frac{1}{10000}$ of a millimeter of blood. This mixture of blood and salt solution is then forced out on an object glass (Fig. 58, C), which under the microscope is seen to be divided into ten squares, each of which when covered by the compressorium (Fig. 58, D)

Fig. 57.



Mixer.

Fig. 58.



Graduated moist chamber with compressorium.

has a capacity of the $\frac{1}{100}$ of a millimeter. Each square will then contain the $\frac{1}{100}$ of a millimeter of the mixture, and consequently will contain the $\frac{1}{100}$ of $\frac{1}{100}$ or the $\frac{1}{10000}$ of a millimeter of blood. Further, as each square is subdivided into twenty smaller squares, the object is to facilitate the counting of the corpuscles. Suppose now, for example, that twenty-five corpuscles could be counted on each of the small squares, then the large square would contain 500 corpuscles; but as the large square contains only the $\frac{1}{10000}$ of a millimeter of blood, it follows that one cubic millimeter will contain $500 \times 10{,}000$, or 5,000,000 corpuscles.

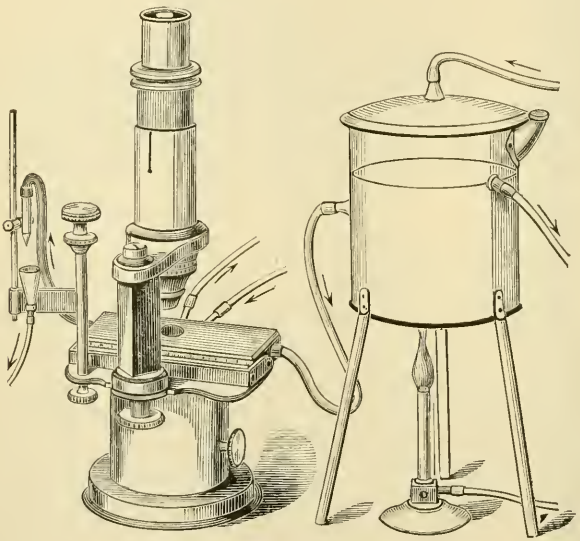
The division of the object glass into ten squares is to enable one to make ten independent observations, so as to obtain an average result. A cubic inch of blood, holding over 70,000,000,000 red blood corpuscles, will contain, therefore, according to Huxley,[1] more than eighty times the number of people upon the globe.

The number of red corpuscles varies, however, not only with the sex as just mentioned, but according to other conditions. Thus, for example, the number of red corpuscles is greater in the adult than in youth, or in old age, in the sanguineous than in the lymphatic temperament, in plethoric than in anæmic persons or in those who have lost blood or who have been deprived

[1] Elementary Physiology. London, 3d ed., p. 78.

of food. Accordingly to Bakewell,[1] race exerts an influence, the number of corpuscles differing in the blood of the Mohammedan, Hindoo, and Negro. Recent investigations appear to show that altitude influences in a marked degree the number of red corpuscles. Thus, according to Vianet[2] a residence in the mountains at a height of 4,932 meters (about 16,000 feet) during two weeks will increase the number of red corpuscles from 5,000,000 to more than 7,000,000 per cubic millimeter, 8,000,000 even being produced after a sojourn of three weeks.

Fig. 59.



Stricker's warm stage.

The specific gravity of the corpuscles is a little higher than that of the liquor sanguinis, being about 1.085. We shall see hereafter that it is for this reason that if blood be allowed to flow into a vessel, coagulation being retarded or prevented, that the corpuscles will tend to settle at the bottom, the plasma being left as a clear supernatant layer.

On observing the corpuscles in blood removed from the body, it will be noticed that soon a number of them run together, forming a chain-like rouleaux of coin (Fig. 54). This is due, according to Robin,[3] to an exudation from the corpuscles themselves which causes them to adhere to each other. Shortly after the blood is drawn the corpuscles will exhibit also small prominences on their

[1] Med. Times and Gazette, Lond., Nov., 1872, p. 514.
[2] La Semaine Medicale, 1890, p. 464.
[3] Journal de la Physiologie, Tome i., p. 295. Paris, 1858.

surfaces, giving them a raspberry-like appearance, and as they become dry they shrivel up and their edges become crenated (Fig. 54). The shape of the corpuscles, however, can be restored even after the lapse of months and years by treating them with a fluid of the density of serum (1.028). This fact is important, from a medico-legal point of view, in reference to determining whether a stain upon clothing or floors, etc., is blood.

The corpuscles swell up and dissolve when pure water is added to them, and acetic acid and other acids have the same effect.

Under the influence of alkalies the corpuscles instantly swell up, appear to burst, and then entirely disappear. The effect of heat is to produce in them bud-like processes. In studying the effects of such reagents as those just mentioned, as well as others, the apparatus represented in Fig. 59, which is to be placed on the stage of the microscope, will be found useful. It consists of a brass box opening laterally by two tubes, with a solid rod-like projection in the middle, and perforated in the center. The central aperture can be converted into a chamber by cementing to its lower opening a cover glass. Surrounding this central chamber is coiled the bulb of a thermometer, whose registering surface is attached externally to the side of the box.

By connecting one of the lateral apertures opposite the projecting rod of the box with the reservoir of hot water and the other with a waste pipe a constant flow of hot water through the brass box is insured, and the temperature of the central chamber regulated as desired by the thermometer.

By screwing on to the rod-like projection of the brass box a rod of the same metal and heating its free end by a spirit lamp, the temperature can also be elevated as required.

If it is desired to study the action of water upon the blood corpuscles, for example, the apparatus is used in the following way: A drop of water is placed on the floor of the chamber, and a drop of blood, usually diluted with salt solution, upon a cover-glass; the latter is then placed inverted over the chamber, the edges of which have been previously oiled or surrounded with a ring of putty, so as to make the chamber air-tight. By allowing the hot water to flow through the brass box, or heating the end of the rod by the spirit lamp, the drop of water on the floor of the chamber is made to evaporate, and, condensing on the under surface of the cover-glass, gradually affects the blood corpuscle it meets there.

The effects of heat simply upon the blood corpuscles can be studied by placing the blood to be examined upon a cover-glass, and dropping this upon another glass of the same size, the edges of which have been previously smeared with oil, and then placing the two glasses with the blood and oil so enclosed over the opening of the chamber. Further, by means of the tubes which open into the chamber, a current of gas can be made to pass through the latter, and its effects studied upon the blood placed upon a cover-glass and

inverted over the chamber, in the manner just described in studying the effect of water.

The effect of electricity upon the corpuscle is to convert it temporarily into rosette-, mulberry-, and finally horsechestnut-shaped forms. To demonstrate this effect, we usually make use of the electrical microscopic stage, placing the drop of blood upon the slide in such a position that when covered it spreads out between the two poles of tinfoil, which are about six millimeters apart and connected either with a Leyden jar having a surface of 500 square centimeters, or by a Du Bois Reymond inductorium fed by a single Bunsen cell, according to the kind of electricity to be used.

According to the high authority of Gulliver,[1] the average diameter of the red blood corpuscle is the $\frac{1}{3200}$ of an inch, with an average thickness of about the $\frac{1}{12400}$ of an inch. The diameter, however, varies as much as from the $\frac{1}{4000}$ to the $\frac{1}{2800}$ of an inch.[2] The importance of remembering these variations will be seen presently.

BLOOD CORPUSCLES.[3]

Mammals.

Animal.	Diameter.
Manatee	$\frac{1}{2700}$ of an inch.
Elephant	$\frac{1}{2745}$ " "
Ant-eater	$\frac{1}{2769}$ " "
Sloth	$\frac{1}{2865}$ " "
Whale	$\frac{1}{3099}$ " "
Camel	$\frac{1}{3123}$ " "
Man	$\frac{1}{3200}$ " "
Orang	$\frac{1}{3383}$ " "
Chimpanzee	$\frac{1}{3412}$ " "
Dog	$\frac{1}{3542}$ " "
Opossum	$\frac{1}{3557}$ " "
Rabbit	$\frac{1}{3607}$ " "
Black Rat	$\frac{1}{3754}$ " "
Mouse	$\frac{1}{3814}$ " "
Brown Rat	$\frac{1}{3911}$ " "
Gray Squirrel	$\frac{1}{4000}$ " "
Ox	$\frac{1}{4267}$ " "
Cat	$\frac{1}{4404}$ " "
Sheep	$\frac{1}{5300}$ " "
Goat	$\frac{1}{6366}$ " "
Pigmy Musk Deer	$\frac{1}{12325}$ " "

[1] In Works of William Hewson, Sydenham edition, p. 237. London, 1846.

[2] In many physiological treatises the diameter of the red blood corpuscle in man is given as $7.7\,\mu$. To the author at least, the statement that the red blood corpuscle measures 0.0077 mm. ($\frac{1}{3200}$ of an inch) is preferable, as being more intelligible to the ordinary, as well as to the scientific, understanding, involving but one mental operation. To state such measurement as being $7.7\,\mu$ involves three distinct mental operations as follows: 1st. $\mu = 0.001$ of a millimeter; 2d. $7.7\,\mu = 7.7 \times 0.001$ mm.; 3d. 7.7×0.001 mm. $= 0.0077$ mm. That the above calculation is necessary, any one will realize who endeavors to picture to himself the diameter of the red blood corpuscle simply in terms of $7.7\,\mu$.

[3] Drawn up principally from table of Gulliver, op. cit., p. 237.

Animal.	Diameter.
Birds.	
Ostrich	$\frac{1}{1649}$ of an inch.
Owl	$\frac{1}{1763}$ " "
Swan	$\frac{1}{1806}$ " "
Pigeon	$\frac{1}{1973}$ " "
Reptiles.	
Turtle	$\frac{1}{1231}$ " "
Viper	$\frac{1}{1274}$ " "
Lizard	$\frac{1}{1555}$ " "
Amphibia.	
Aphiuma	$\frac{1}{363}$ " "
Proteus	$\frac{1}{400}$ " "
Siren	$\frac{1}{420}$ " "
Menopoma	$\frac{1}{363}$ " "
Fishes.	
Pike	$\frac{1}{2000}$ " "
Perch	$\frac{1}{2000}$ " "
Lamprey	$\frac{1}{2134}$ " "

While there is not always a proportional relation between the size of the blood corpuscle and that of the animal—that of the ox, for example, being smaller than that of man or the dog—Milne Edwards[1] has shown, by a comparison of the size of the blood corpuscle in the five classes of vertebrates, that there does exist a most remarkable connection between the size of the corpuscle and the degree of nervo-muscular power of the animal; the corpuscles being small in the most highly developed and active vertebrates, and large in those least so. It will be seen also, more particularly, that the size of the corpuscle is most intimately related to the activity of the respiration, the corpuscle being smallest in those animals whose respiration is the most active, and largest in those in which this function is slow. This might be expected, as a large number of small corpuscles offer a larger absorbing surface to the oxygen, the respiratory element, than a small number of large ones. As we proceed we shall see that muscular is largely dependent upon respiratory activity. Hence, if the above view be correct, we should expect to find the blood corpuscles smallest in the active vertebrates and largest in the sluggish ones.

On comparing the size of the blood corpuscles in the mammalia with those of the reptilia or batrachia, we find such to be the case. Of course, if this comparison be carried out to extreme detail, there will be found exceptions to the rule, for no doubt other conditions beside those of respiration influence the size of the corpuscles, possibly the character of the food, etc.; but that the connection just referred to is something more than mere coincidence seems to be fully justified by Milne Edwards's elaborate survey of the facts.

[1] Physiologie, Tome i., p. 57.

It will be seen that there are a few mammals in which the blood corpuscles are larger than those of man, and that the blood corpuscle of the pigmy deer (Tragulus) is the smallest known, while those of a batrachian, the amphiuma, are the largest.

The exact size of the red blood corpuscle in man is not only of interest physiologically, but also from a medico-legal point of view.[1] Attention has already been called to the fact that there is a considerable variation in the size of the human corpuscles, and hence it is often impossible to say positively whether a given corpuscle came from a human being's blood or that of an ape, dog, rabbit, rat, mouse, or ox, for the average diameter of the corpuscles in these animals is within the limits of the variations that have been mentioned as occurring in man.

When a large quantity of human blood is examined, probably ninety-five corpuscles out of every hundred will exhibit the same diameter, but in a medico-legal investigation the amount of blood put at the disposal of the expert is often exceedingly small—an old blood stain, a single drop, perhaps, and possibly the variable corpuscles contained in this very drop. Now, as the size of the corpuscle in the dog or the ox varies as well as that of man, if the size of the corpuscle in the suspected fluid is only taken into consideration, the blood of a dog might be determined to be that of a man, and *vice versâ*. In fact, it is impossible to say beyond the shadow of a doubt that a given drop of liquid is human blood and not that of the animals referred to above, for the small size of the variable human corpuscle might lead the examiner to think the human blood had come from a dog or a mouse, while from the variable large corpuscles in the blood of these animals there might be a suspicion that their blood was human.

With the exception of the camel and llama, in which the red blood corpuscles are oval, the form of these bodies in the mammalia thus far examined is circular, which adds to the difficulty of distinguishing the blood of the domestic mammals from that of man. On looking at Fig. 60, it will be seen that the red blood corpuscles in birds, reptiles, batrachia, and fishes differ from those of man and the mammalia generally in being oval in form and in exhibiting a well-marked nucleus, and in being much larger.

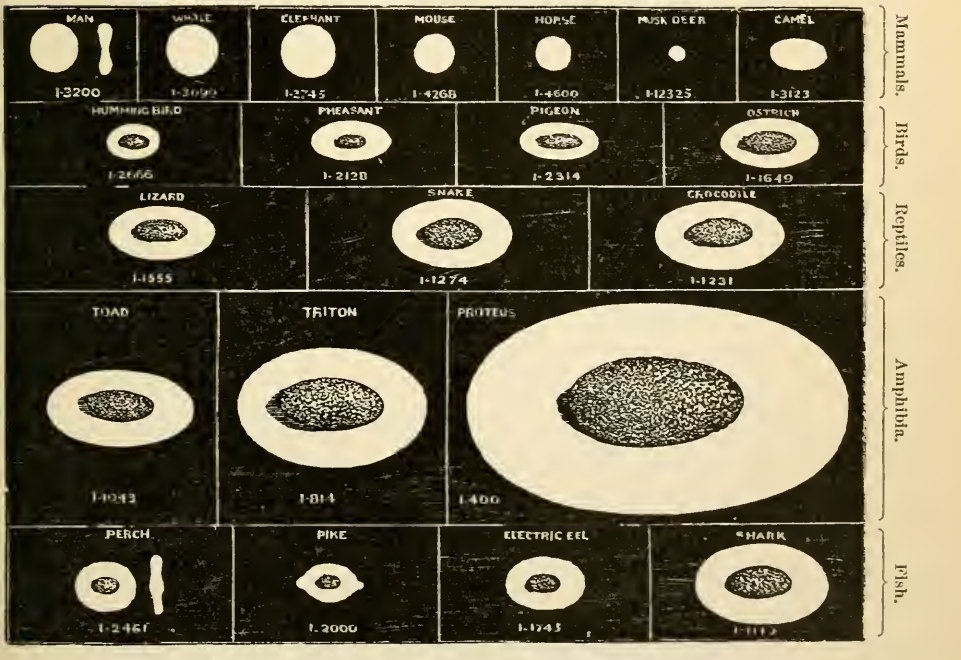
The only partial exceptions to the above statement are offered by the oval corpuscles of the dromedary and llama; but, as will be seen from Fig. 60, they are not nucleated. At the other end of the vertebrate series we find a further exception, in the nearly circular corpuscles of the lamprey, but these are nucleated. There can be no difficulty, therefore, in distinguishing the blood corpuscles of the birds, reptiles, etc., from those of mammals. The oval form, and the presence of a nucleus, especially, are sufficient to decide positively that the blood containing such corpuscles is not

[1] For the method of measuring the blood corpuscles, the reader is referred to the Author's Manual of Medical Jurisprudence, 2d edition, 1896, p. 66.

mammalian. Such knowledge has been of advantage more than once in assisting in the detection of murder.

The most important use of the red blood corpuscles is undoubtedly as carriers of oxygen. Blood will absorb ten to thirteen times as much oxygen as water, this function depending entirely, as we shall see presently, upon the hæmoglobin of which the corpuscles largely consist. In concluding our account of the red blood corpuscles, let us briefly consider their origin, at least so far as is known, for there is no doubt their life is of limited duration. Abundant evidence of the disintegration of the red blood corpuscles is seen in different parts of the economy, their coloring matter more

FIG. 60.



Typical character of red blood cells of vertebrata. (KIRKES.)

or less broken down is found, for example, in the liver and spleen, and which we shall see hereafter, gives rise to the biliary and urinary pigments. There appears to be but little doubt that in the adult the formation of red corpuscles or hæmatopoiesis, as the process is called, takes place in the red marrow of the cancellous tissue of bones,[1] the corpuscles being developed out of the colorless nucleated cells of the latter.

The erythroblasts, as these cells are called, are supposed to multiply by karyokinesis, the daughter cells so produced, then elabo-

[1] Neumann, Archiv der Heilkunde, Zehnter Jahrgang, 1869, s. 220. Bizzozero, Centralblatt für die Medicinischen Wissenschaften, Sechster Jahrgang, 1868, s. 885.

rate hæmoglobin in their cytoplasm, and subsequently in losing their nucleus become red corpuscles, which, in turn, pass into the general circulation. In the fœtus, however, the liver and spleen take an active part in hæmatopoiesis. It is quite probable, therefore, that they may still in the adult exert some influence in the production of red blood corpuscles, as well as the red marrow. It may be mentioned in this connection that at the end of the third month of fœtal life three-fourths of the red blood corpuscles are still nucleated. As development advances, however, the latter steadily diminishes in number until they finally disappear, being replaced by the non-nucleated ones of adult life. As the properties of the red blood corpuscles that still remain to be described depend upon the hæmoglobin that they contain, their further notice will be deferred until the subject of hæmoglobin is especially considered.

CHAPTER XI.

THE BLOOD.—(*Continued.*)

THE white corpuscles discovered by Hewson[1] about 1770, as their name implies, are of a grayish, whitish color, of a round form, and consist of a mass of protoplasm containing granules. A cell wall cannot be said to exist. Chemically the white corpuscles are composed of proteid substances, lecithin, glycogen, salts, fat, cholesterin.[2]

When the blood is maintained at the temperature of the body the form of the white corpuscle is seen under the microscope to be constantly changing, alternately protruding and retracting its body substance in an amœbiform manner (Fig. 61). By adding finely

FIG. 61.

Various forms assumed by the white corpuscles of the blood. The upper row represents the white corpuscles of man; the lower row, white corpuscles from the newt, showing changes effected in fifteen minutes. (CARPENTER.)

powdered indigo to serum containing white corpuscles the manner in which they feed can be observed, the indigo being drawn into the body of the corpuscle by the retraction of its amœba-like arms and then gradually absorbed and assimilated.

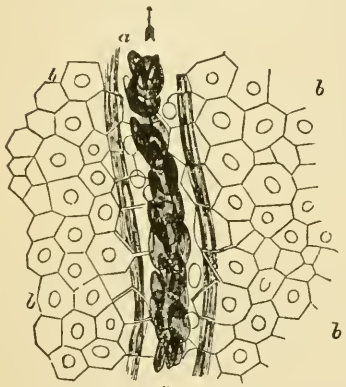
The white blood corpuscles not only have the power of protruding and retracting their arms, but, like the amœba itself, can move from place to place, and at times may even pass through the walls of the blood capillaries into the surrounding tissues, hence the name of "wandering cells," sometimes given to them.

The white corpuscle is larger than the red one, measuring on an average the $\frac{1}{1000}$ of a millimeter ($\frac{1}{2500}$ of an inch). The white corpuscles are far less numerous than the red ones, being found usually

[1] Works, p. 282. [2] Hoppe-Seyler, Untersuchungen, Band iv., s. 441.

in the proportion of one white corpuscle to between 300 and 500 red ones. This proportion, as we learn, however, from the observations of Hirst,[1] varies according to the state of digestion: thus before breakfast the proportion being about 1 to 1800, one hour after breakfast it was 1 to 700, before dinner 1 to 1500, after dinner, 1 o'clock, 1 to 400, two hours later 1 to 1475, after supper, 8 P. M., 1 to 550, at midnight about 1 to 1200. The white corpuscles differ also in many other respects from the red ones: thus in the manner in which they are affected by various reagents, and in the way in which they adhere to the walls of the vessels in which they are circulating (Fig. 62), the red corpuscles keeping in the middle of the stream.

FIG. 62.



A small venous trunk, *a*, from the web of the frog's foot. *b*, *b*. Cells of pavement-epithelium, containing nuclei. *d*. White corpuscles. *e*. Red corpuscles. (CARPENTER.)

The white corpuscles are found also in lymph, chyle, pus, and other fluids as well as in the blood; the more general name of leucocytes is often therefore given to them. It should be mentioned that many histologists consider the leucocytes or white blood corpuscles as being of three kinds. It is claimed by those holding this view that the white corpuscles differ from each other in the manner in which they stain with acid, basic, and neutral dyes, or according to the number of the nuclei they may contain, or to the amount of amœbiform movement they may exhibit. It is very probable, however, that the three different kinds, so called, are only different stages of development of one kind of white corpuscle, and for the present, at least, they will be so regarded. The white blood corpuscles originate apparently in the lymphatic glands and in the lymphoid tissue of the body, generally, whence passing into the lymph they are carried into the blood. As a confirmation of this view, attention may be called to the fact that in disease of the spleen and lymphatic glands the white corpuscles may increase in number to such an extent as to form a third or even a half of the corpuscular part of the blood. Hence the light color of the blood in such circumstances and the name of the disease—leucocythemia.

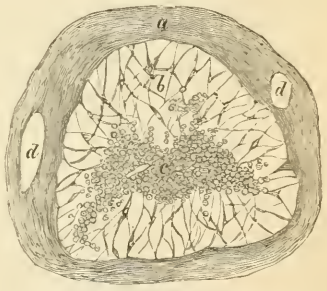
To a certain extent at least, however, the white blood corpuscles appear to be reproduced in the blood itself by karyokinesis. At one time it was supposed that the white corpuscles in the course of development elaborated red coloring matter within their protoplasm, lost their nuclei, and finally became, very much in the same man-

[1] Muller's Archiv, 1856, s. 174. Lilienfeld. Du Bois Reymond, Archiv, 1893, s. 560.

ner as the erythroblasts, red corpuscles. Much indeed might still be said in favor of this view, many of the facts of comparative anatomy, embryology, and pathology apparently supporting it. It must be admitted, however, that as yet we do not know positively what becomes of the white corpuscles, whether they are transformed into some other kind of corpuscles, or, having played their part in the economy, simply disintegate. Various functions have been assigned to the leucocytes generally. It has been held that they promote the absorption of fats and peptones from the intestine, that they constitute one source of supply of proteid material to the blood, and of the fibrin ferment, one of the supposed factors in the coagulation of the blood, that they are phagocytes and in feeding upon pathogenic bacteria protect the body from the attacks of the same, etc. Until, however, the life history of the white blood corpuscles is known from beginning to end, their uses must be to a great extent as much a matter of speculation as their fate.

It has already been mentioned that the white corpuscles are not confined to the blood, being also found in the lymph, chyle, solitary and lymphatic glands, and in the spleen.

FIG. 63.



Simple lymphatic gland. *a*. The capsule with sections of lymphatics, *d*, *d*. Coursing through it. *b*. Lacunar and intercommunicating passages, permeated by the lymph, and forming the superficial lymph-path of Frey. *c*. Nucleus or medullary portion of the gland, in the center of which the section of a blood vessel may be seen. The path pursued by the lymph through the medullary portion constitutes the deep or secondary lymph-path of Frey. (CARPENTER.)

The solitary glands, as we have already noticed, are distributed all through the alimentary canal; the Peyer's patches, which consist of a number of solitary glands united together, are, however, limited to the so-called jejunum and ileum. When a section of one of these solitary or simple lymphatic glands is examined microscopically (Fig. 63) it is seen to consist of a capsule of connective tissue from which pass inwardly strands forming a meshwork, in the interior of which is contained the so-called adenoid or cytogenous tissue. These strands of connective tissue serve to support the capillary blood vessels. In the meshes are found lymph corpuscles and sometimes molecular granules and small oil globules. The lymphatic differs from the solitary gland in that its meshwork being denser in the middle than at its sides, the distinction of the medullary and cortical parts is better marked (Fig. 64). Further the meshes in the lymphatic gland are only incompletely filled by the pulp, free spaces being left between the pulp and the strands. These spaces communicate on the one hand with the lymphatic vessels entering the gland, and on the other with the lymphatics leaving it at the hilus. The afferent and efferent lymphatic vessels and these spaces can be injected. Probably this is the explanation of the

gland appearing after injection as a mass of vessels, a rete mirabile between and continuous with the lymphatics passing in and out of it. The pulp consists principally of lymph corpuscles, these being most numerous in the medullary parts of the gland, where the blood vessels are also freely distributed.

The lymph or chyle passes from the afferent vessels into the spaces left between the pulp and the strands, and comes in contact with the lymph corpuscles and the blood, more particularly in the medullary parts of the gland; after circulating through these spaces the lymph or chyle passes out of the gland at the hilus by the efferent lymphatic vessels, and so passes on to the thoracic duct.

Fig. 64.

Section of lymphatic gland, showing *a*, *a*, the fibrous tissue which forms its exterior. *b*, *b*. Superficial vasa inferentia. *c*, *c*. Larger alveoli, near the surface. *d*, *d*. Smaller alveoli of the interior. *e*, *e*. Fibrous walls of the alveoli. (Carpenter.)

The researches of Klein,[1] von Recklinghausen,[2] and others have shown that the walls of the serous sacs, like the peritoneum, pleura, etc., consist, to a considerable extent, of the adenoid or cytogenous tissue just mentioned, which enters into the formation of the solitary and lymphatic glands, and that these serous sacs communicate by openings or stomata with the lymphatics. The tonsils also appear to consist essentially of nodular masses of lymphoid tissue embedded in the submucosa of follicles of the mucous membrane.

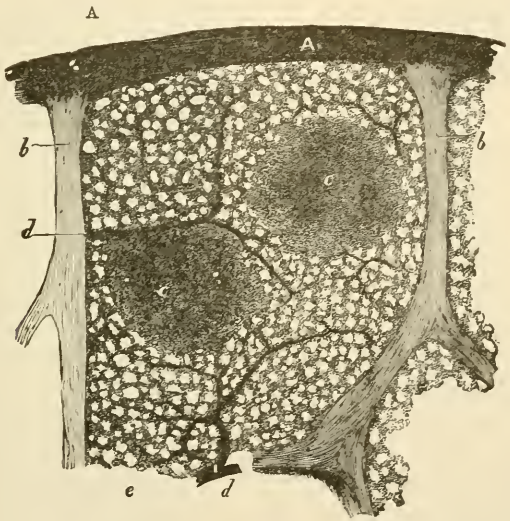
We have already seen that the lymph differs from the blood quantitatively, rather than qualitatively, and that the chyle is lymph with the products of digestion added to it, more especially of the emulsified fats and oils. The lymph and chyle corpuscles, which are indistinguishable from the white corpuscles of the blood, seem to consist at first of fatty nuclei, which, acquiring an envelope through diffusion in an albuminous fluid, gradually become white corpuscles. In examining the chyle of the lacteals in the villi, in the mesenteric glands, and in the thoracic duct, it was noticed that the so-called molecular base of the chyle consisted largely of fatty matter, and that the chyle corpuscles were probably due to an aggregation of the minute bodies forming the base of the chyle. It seems probable, therefore, that the chyle corpuscles, or white corpuscles of the blood, are elaborated in the lymphatic glands.

In addition to containing white corpuscles, the chyle resembles an early stage of the blood in other respects, thus between the mesenteric glands and thoracic duct it will coagulate—that is, separate into clot and serum, while the chyle of the thoracic duct exhibits a reddish color.

[1] Anatomy of the Lymphatic System, 1873. [2] Stricker's Histology, p. 215.

Spleen.—In examining the structure of the spleen one cannot but be impressed with its great similarity to a lymphatic gland. Like the lymphatic gland, the spleen (Fig. 65) consists externally of a fibrous capsule, from which pass inward numerous strands, constituting the so-called trabeculæ, in the meshes of which is contained the splenic pulp. This consists of white blood corpuscles, of red corpuscles in various stages of development or disintegration, of granular matter of a reddish-brown hue, blood crystals, iron, etc. The only difference between the spleen and a lymphatic gland consists in the fact that the cells found in the spleen pass directly into the blood.

FIG. 65.



Vertical section of a small superficial portion of the human spleen. Low power. *A*. Peritonea and fibrous covering. *b*. Trabeculæ. *c, c*. Malpighian corpuscles, in one of which an artery is seen cut transversely, in the other longitudinally. *d*. Injected arterial twigs. *e*. Spleen-pulp (KÖLLIKER.)

That the spleen is essentially a lymphatic gland seems confirmed by the fact that when it is small in man or an animal, the lymphatic glands are large, and *vice versâ*. Not only is this inverse ratio observed in the same animal but also in different species. Thus, among other instances observed by the author, in the manatee the spleen is very small while the glands are very large, whereas, in the sea lion, the reverse obtains. This view of the nature of the spleen is confirmed by the fact that it can be removed from animals with impunity, the lymphatic glands then enlarging and through vicarious action apparently performing its function, and also that the spleen is absent in the lowest of vertebrates, the amphioxus. On the other hand, with hypertrophy of the spleen, we have, coincidently, disease of the bones indicating the relationship, functionally, between the two. Indeed, recent observations[1] render

[1] Laudenbach, Centralblatt für Physiologie, 1896, Band ix., s. 1.

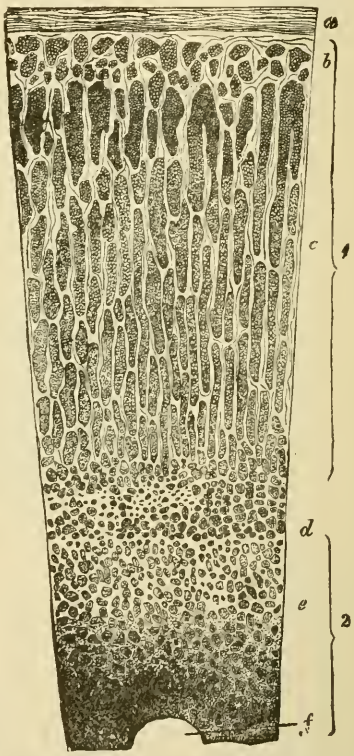
it probable that the spleen produces red blood corpuscles as well as leucocytes which becomes intelligible when it is remembered what has already been said as to the influence of the marrow in hæmatopoiesis.

One of the most striking peculiarities of the spleen is its great vascularity. Not only does a large quantity of blood flow into the organ, but the distribution is remarkable inasmuch as capillaries in certain parts are absent, the blood of the splenic artery passing then directly into the interstices of the pulp to be taken up by the

Fig. 66.

Front view of the right kidney and suprarenal body of a full-grown fœtus. *r*, *r*. The renal vein and artery. *u*. The ureter. *s*. The suprarenal capsule, the letter is placed near the sulcus in which the large veins (*v'*) are seen emerging from the interior of the organ. (Allen Thomson.)

Fig. 67.



Vertical section of suprarenal capsule of man. 1. Cortex. 2. Medulla. *a*. Capsule. *b*. Layer of external cell-masses. *c*. Columnar layer (zona fasciculata). *d*. Layer of the internal cell-masses. *e*. Medullary substance. *f*. Section of a vein. (Carpenter.)

veins, a type of circulation that obtains in the invertebrates. It may be mentioned in this connection that the so-called Malpighian corpuscles attached to the branches of the splenic artery in the spleen do not appear to differ essentially in their minute structure from that of the solitary glands. It is well known that during digestion the spleen slowly increases in size, the maximum being attained about five hours after taking food, the organ then slowly shrinking to its previous size. It has also been shown[1] that the spleen contracts and relaxes in animals in a rhythmical manner about once in a minute, the movements being apparently due to the muscular tissue of the capsule and trabeculæ. These facts, while interesting, do not throw any light, however, upon the function of the spleen. The spleen

[1] C. S. Roy, Journal of Physiology, 1881, Vol. iii., p. 203.

is richly supplied by branches from the splanchnic nerves which appear to contain both vaso constrictor and dilator fibers.[1]

Suprarenal Capsules.—These bodies (Fig. 66), often also called adrenals, resemble in many respects, in their intimate structure, lymphatic glands. Like the latter, they consist (Fig. 67), to a great extent, of trabeculæ, in the ovoid meshes of which are imbedded cells, with and without nuclei, containing granules, oil, and pigmentary matter. The immense number of nerves distributed to the adrenals is one of their most remarkable peculiarities. The suprarenal capsules appear to be essential to the nutrition of the human economy, since their removal in animals causes death in a day or two, or even in a few hours.[2] The symptoms preceding death in these cases, such as great prostration, muscular weakness, loss of vascular tone, closely resemble those of Addison's disease in man, due to pathological changes arising in the adrenals. From the fact that removal of the suprarenal capsules in animals is followed by death and that Addison's disease in man is benefited, to some extent at least, by the use of adrenal extracts, it has been inferred that the suprarenal capsules elaborate some material, an internal secretion, which, passing into the blood, profoundly influences nutrition. Recent researches[3] render it probable that the material so elaborated acts more especially upon the vascular and muscular system, stimulating both striated and unstriated muscular fibers. Injections of the medullary part of the suprarenal capsules into the veins of an animal, for example, prolong the contractions of the heart, increase blood pressure by constricting the arterioles, and stimulate the muscles generally to great activity.

Thyroid Body.—The functions of the thyroid glands, or the thyroid body as it is often called in man, on account of the glands being united in the latter by a band or isthmus lying in front of the trachea, may be appropriately considered in this connection, as they appear to influence, to some extent at least, hæmatopoiesis. The thyroid glands, relatively larger in the fœtus and in the infant than in the adult, measure in the latter condition about 50 millimeters (2 inches) in length and 30 millimeters (1.2 inches) in breadth. They consist of closed vesicles of variable size, imbedded in a connective tissue which supports a network of blood vessels and lymphatics. The vesicles (Fig. 68) are lined with a single layer of cuboidal epithelial cells, and appear to secrete the glairy colloidal fluid found not only within the cells, but between them. It is well known that the profound disturbance in nutrition following the removal of the thyroid glands in man or of the thyroid accessory, thyroid and parathyroid glands in animals[4] is so great as to soon cause death. It ap-

[1] Schaefer, Proc. Royal Society, 1896, Vol. lix., No. 355.

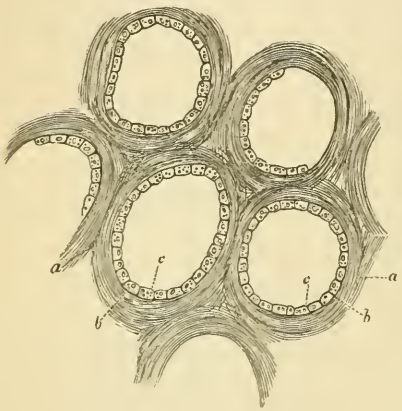
[2] Brown Sequard, Comptes rendus de l'Ac. des Sciences, Tome xliii., 1856, pp. 422, 542. Szymonowicz, Pflüger's Archiv, Band lxiv., 1896, s. 97.

[3] G. Oliver and E. A. Schäfer, Journal of Physiology, xviii., 1895, p. ix. Cybulski and Szymonowicz, Jahresberichte Über Die Fortschritte der Thier Chemie, 1895, s. 379.

[4] Schiff, Untersuchungen über Die Zuckerbildung In der Leber, etc., Würzburg,

pears to be well established that the spasms, convulsions, emaciation following extirpation of the thyroids, the symptoms of myxœdema, cretinism, cachexia, thyreopriva and thyreoidectomica cannot only be greatly relieved, but death averted by injecting thyroid extracts, feeding with the fresh gland or even by grafting part of the gland under the skin.[1] Such being the case it would appear that the thyroid glands richly supplied with blood elaborate from the latter a material which, passing into the lymph and thence into the blood, promotes the general nutrition of the body, possibly by increasing the number of red corpuscles,[2] or by destroying some toxic substance, the accumulation of which in the system gives rise by autointoxication to the symptoms following thyreoidectomy and cachexia thyreopriva. While the composition of the colloidal secretion of the thyroid glands is as yet only imperfectly known, recent researches render it highly probable that its most active constituent is thyroiodin, or iodothyrin as it is also called,[3] which exists in the glands in combination with proteid material, and is characterized by the great resistance it offers to the action of ordinary chemical agents. To this colloidal substance thyroiodin must be attributed to a great extent at least, the benefit derived from thyroid extracts, etc., as administered in thyroid therapy.[4] That the thyroid glands have the function of elaborating an "internal"[5] secretion essential to nutrition, as held by the older physiologists,[6] is rendered also probable from the fact as we have seen of the liver and pancreas elaborating internal secretions such as glycogen, urea, and a glycolytic ferment respectively.

FIG. 68.



Group of gland-vesicles from the thyroid gland of a child. *a*. Connective tissue. *b*. Membrane of the vesicles. *c*. Epithelial cells. (CARPENTER.)

1859, s. 61. Gley, Archives de Physiologie Normal et Pathologique, 5 Serie, Tome iv., 1892, pp. 135, 311, 664. Christiani, Ibid., 1893, p. 39. Vasale et Generali, Archives Italiennes, De Biologie, Tome xxv., 1896, Fas. III., p. 459.

[1] Kocher, Bucher, Horsley, Murray, Howitz referred to by Lauzon, Klinische Vorträge, 1894.

[2] Chittenden, Science, June, 1897, p. 5.

[3] Baumann und Roos, Zeitschrift für Physiol. Chemie, Band 21, 1896, s. 319, s. 481, Band 22, 1896, s. 1. Hutchinson, Journal of Physiology, Vol. 20, 1896, p. 474.

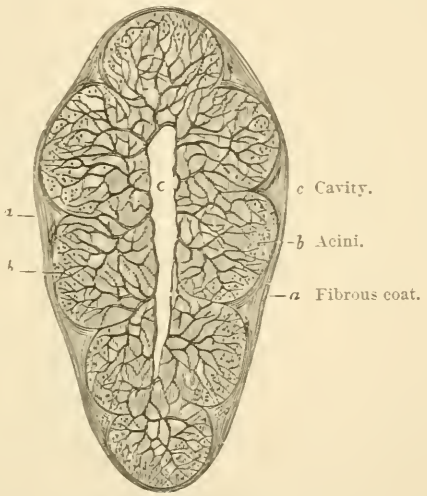
[4] Ewald, Verhandlungen des Congresses für innere Medecin, 1896, s. 101.

[5] Bernard, Rapport sur les progrès et la marche de la Physiologie générale en France, 1867, p. 69.

[6] Haller, Elementa Physiologiæ, Tomus iii., 1766, p. 400: "Liquorem peculiarem in ea glandula parari, qui receptus venulis sanguini reddatur, quæ etiam lienis & thymi sit utilitas, ipse Ruyschius Autumavit."

The Thymus Gland.—The thymus gland appears in the embryo first as a solid body, but soon becomes a tube closed at both ends and filled with granular matter. From this tube (Fig. 68) there bud out at intervals, on either side, hollow lobular processes, the cavities of which communicate with that of the central axis. The thymus in the adult consists of a series of such offshoots or lobules united by connective tissue and opening into the central tube, to which, however, there is no outlet. Each lobule (Fig. 69) consists

FIG. 69.



Section of lobule of thymus.

of an external fibrous capsule which sends prolongations into its interior consisting of acini, in the meshes of which are seen the thymus substance. This contains lymph corpuscles, spheroidal granular bodies, and concentric corpuscles. In the expressed thymus juice are found corpuscles which are indistinguishable from those of the fluids of the lymphatic glands. The thymus gland, in its whole structure, resembles very much a Peyer's patch. The functions of the thymus gland are unknown. It is possible that it elaborates, like other ductless glands, an internal secretion that in some way promotes nutrition, and especially in early life, since it diminishes in size after puberty.

The blood contains, as already mentioned, in addition to the red and white corpuscles, other formed elements, the blood plates of Hayem.[1] These are minute bodies, though attaining sometimes a size of the $\frac{1}{180}$ of a mm. ($\frac{1}{4500}$ of an inch) in diameter, circular in form and homogeneous in structure. Much difference of opinion still prevails among histologists as to the nature of the blood plates.

[1] Comptes Rendus, T. 86, p. 58, 1878.

Some regard them as a distinct, third kind of corpuscle, others as only the nuclei of the disintegrated leucocytes. The latter view is based not only upon morphological grounds but upon the fact of the blood plates containing the same kind of nucleo-albumin [1] as the nucleus of the leucocytes. Apart from contributing nucleo-albumin to the blood whose significance is speculative and of the supposed use in the production of the fibrin ferment, the function of the blood plates is entirely unknown.

[1] Lilienfeld, Du Bois Reymond, Archiv für Physiologie, 1893, s. 560.

CHAPTER XII.

THE BLOOD.—(*Continued.*)

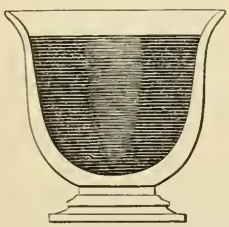
One of the most interesting properties of the blood is its power of coagulation, that is of separating into clot and serum. Before coagulation the blood consists of the liquor sanguinis or plasma and the corpuscles; after coagulation it will be found that the corpuscles are entangled in a fine network consisting of the meshes of the coaguated fibrin, the two constituting the clot or crassamentum, while the proteids, salts, and water remain together as the serum. It is important to notice that the liquor sanguinis, or the plasma, is not identical with serum, liquor sanguinis being serum with the addition of fibrinogen, serum liquor sanguinis without fibrinogen. Serum differs also from what are known as serous effusions, which are due to transudations, not to coagulation.

BLOOD.

Before coagulation.		After coagulation.
Liquor sanguinis.	Water	Serum.
	Salts	
	Proteid	
	Fibrinogen	Clot.
Corpuscles	. . . . .	

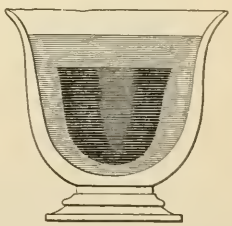
When the blood is allowed to flow into a tolerably deep, smooth vessel, according to Nasse,[1] in from about one minute and forty-five seconds to six minutes a gelatinous layer will be seen to form on its surface; in from two to seven minutes the sides of the vessel are covered with a similar layer, and in from seven to sixteen minutes

Fig. 70.



Bowl of recently coagulated blood, showing the whole mass uniformly solidified. (Dalton.)

Fig. 71.



Bowl of coagulated blood, after twelve hours showing the clot contracted and floating in the fluid serum. (Dalton.)

the whole of the blood becomes jelly-like (Fig. 70); gradually there exudes from the contracting jelly-like mass, drop by drop, a

[1] Wagner, Physiologie, 1842, Band i., s.104.

fluid, the serum, and in from ten to twelve hours the coagulation is complete—that is, the separation of the blood into clot and serum (Fig. 71). The contracted jelly-like red mass, the clot, being heavier (specific gravity of corpuscles, 1.088), usually falls to the bottom of the straw-colored or reddish liquid, the serum (specific gravity, 1.028), surrounding it, and which has exuded from it.

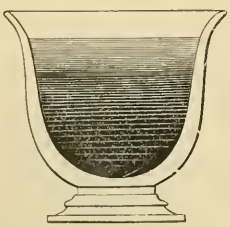
Usually, according to Milne Edwards,[1] the clot retains about one-fifth of the entire volume of the serum; this should be remembered when the proportion of clot to serum is estimated; it being generally stated that they are equal. When the coagulation has been slow, the clot will be found to be firm; on the other hand, when the coagulation has been rapid the clot is soft. When the blood coagulates slowly, and so remains fluid for some time, the red corpuscles, on account of their weight, sink and settle at the bottom of the clot; the upper part of the clot will be, therefore, much lighter in color than the lower, and, when white, is known as the buffy coat (Fig. 72); it is almost always seen in the blood of the horse, which coagulates slowly, while it is absent in the pigeon, in which the blood coagulates almost instantaneously.

LENGTH OF TIME OF COAGULATION.[2]

Animal.	Minutes.	Animal.	Minutes.
Man	2 to 16	Rabbit	½ to 1½
Horse	5 to 13	Lamb	½ to 1
Ox	2 to 12	Duck	½ to 2
Dog	½ to 3	Fowl	½ to 1½
Sheep	½ to 1½	Pigeon	almost instantaneously.
Hog	½ to 1½		

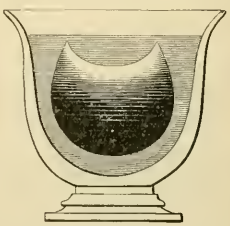
When contraction of the clot takes place most rapidly at the edges, these curl up and the upper surface becomes concave or cupped (Fig. 73). For many years it was supposed that the buffy coat

FIG. 72.



Vertical section of a recent coagulum, showing the greater accumulation of blood globules at the bottom. (DALTON.)

FIG. 73.



Bowl of coagulated blood, showing the clot buffed and cupped.

was characteristic of inflammation, whereas it is now known that the buffy coat is also present in diseases of a totally opposite character—in chlorosis, for example, it depending here upon a diminu-

[1] Physiologie, Tome i., p. 124.
[2] Thakrah, Inquiry into the Nature of Blood, 1819, p. 29.

tion of the blood corpuscles. It is obvious that bleeding in such cases would only increase the buffy coat by diminishing still further the corpuscles, and, when it is remembered that bleeding was once the sovereign remedy for inflammation, one can readily appreciate the number of lives that must have been sacrificed through the mistaken idea of the buffy coat being invariably due to inflammation.

Indeed, the formation of the buffy coat, as shown by the researches of Polli,[1] appears to be simply a question of time, depending upon the coagulation being retarded or accelerated.

It is well known that there are various circumstances which modify the coagulation of the blood. Thus, blood flowing from a small orifice coagulates more quickly than when flowing from a large one, and more quickly when it is received in a shallow rough vessel than when in a deep smooth one. Blood coagulates more rapidly in a vacuum than in the air. Rapid freezing prevents the coagulation of the blood; this will take place, however, after careful thawing. This fact is of importance from a medico-legal point of view.

Elevation of temperature between 0° C. and 60° C. (32° and 140° F.) increases the rapidity of coagulation. Chemical substances, like solutions of sodium and magnesium sulphate, when mixed with blood will retard its coagulation, while sodium or potassium oxalate when added to saturation, as we shall see presently, will prevent coagulation altogether. Menstrual blood, while clotting in the uterus, is kept in a more or less fluid condition in the vagina, by the mucus of the latter. In this connection may be mentioned also the well-known fact as yet, however, unexplained, that human blood will remain in the alimentary canal of the leech for days and weeks without coagulating.

The blood not only coagulates outside the body, but also after death within it; less rapidly, however, and, as a rule, in from twelve to twenty-four hours after death. It is not unusual, also, during life to find clots in the heart and other parts of the vascular system. As it is often important to be able to distinguish an ante-mortem from a post-mortem heart-clot, it may be stated that the former are whiter, denser, and adhere more closely to the walls of the heart than the latter. Coagula are also found when an artery is ligated, in the enlarged veins of hemorrhoids, in the varicose veins of the extremities. Usually the blood coagulates when effused into the areolar tissue or the cavities of the body. It is an interesting fact, however, that the blood may remain fluid in the serous cavities for days and weeks at a time. When coagula are formed in the heart, and being swept into the circulation are carried thence into the small vessels of the brain, etc, they constitute what are known as emboli. When the blood coagulates in the economy it acts as a foreign body, but is usually absorbed, though this may take a long time. The corpuscles first disappear, then the fibrin softens, breaks down, and is finally carried away.

[1] Annali Universali di Medicina, 1843, p. 249.

The coagulability of the blood is nature's cure for hemorrhage, and when this power is diminished or wanting we have the hemorrhagic diathesis, where the slightest wounds are followed by severe, and sometimes fatal, hemorrhage.

From time immemorial various explanations have been offered of the coagulation of the blood. A favorite one has been that of the blood being maintained in the body in a liquid condition through the influence of life. Apart from this being no explanation at all, but simply a statement of the phenomena to be explained, it is not even a fact, as we have seen that the blood coagulates in the living body. In the last century it was generally held that what we call fibrin was produced in some way at the expense of the corpuscles, which run together in coagulation, etc. Petit, Davies, and Hewson,[1] however, held that coagulation was due to some distinct substance independent of either the corpuscles or the serum, and Hewson performed several experiments to prove that coagulation was due to the fibrin. For example, Hewson[2] added a little sodium sulphate to fresh blood, which prevented coagulation. After the mixture had remained standing some time the corpuscles sank to the bottom, the clear fluid which remained on top was then decanted, twice its quantity of water was then added to this, when the fibrin coagulated. On another occasion, this most able observer[3] tied the jugular veins at the sternum of a dog just dead, and hung his head over the edge of a table, so the ligatures might be higher than the head. The upper part of the vein became transparent, the red corpuscles sinking; he then tied the vein, separating the clear from the red part, and let the clear part out, which was fluid, but coagulated soon after. These experiments showed that the coagulation was due to the fibrin, but they did not demonstrate that this fibrin did not come from the corpuscles, which was the view that prevailed at that time. To do this it was necessary to show that the corpuscles were unaffected to coagulation.

With reference to determining this point, Johannes Müller,[4] the great Berlin physiologist, in 1832 experimented in the following ways: He added a little solution of sugar to frog's blood, which retarded the coagulation, and then filtered the mixture; the corpuscles, which are very large, were retained in the filter, and the clear fluid which passed through coagulated. Müller then showed that in blood which was defibrinated by whipping, and therefore incoagulable, that the corpuscles were not altered in any appreciable manner; and further, that when blood to which had been added serum (which separated the corpuscles from each other) was observed under the microscope coagulating, the corpuscles were seen to remain intact.

Inasmuch as the white stringy substance appearing at the moment

[1] Milne Edwards, op. cit., Tome i., p. 119.
[2] Works, p. 12. [3] Ibid., p. 32.
[4] Physiology translated by Baly, 1840, Vol. 1st, p. 123.

of coagulation, which we call fibrin, evidently does not exist as such in the blood before coagulation, it remains to be determined, if possible, under what form it then does exist. If blood be drawn into a concentrated solution of sodium sulphate to prevent its coagulation, and sodium chloride be added to the mixture in the proportion of ten per cent., a whitish, pasty substance is thrown down, amounting to about 25 parts per 1000 of the blood used, and called by Denis,[1] who first described it, plasmin, and which, together with serin, constitutes blood albumin. Now, when plasmin is redissolved in water, the solution splits into fibrinogen 3 parts, and paraglobulin 22 parts, the former coagulating, the latter remaining liquid. It would appear, therefore, that fibrin exists in the blood combined with paraglobulin, as plasmin or some form closely allied to it; and further, as with the withdrawal of the plasmin from the blood, the latter loses its power of coagulating, the serin remaining liquid, that coagulation of the blood consists, first, in the splitting of albumin into serin and plasmin, and secondly, in the latter splitting into fibrin and paraglobulin, or of the breaking up of albumin directly into serin, fibrin, and paraglobulin.

On the other hand, the observation, made many years ago by Buchanan,[2] that two fluids, like that of hydrocele and ascites, or of ascites and pleurisy, when added together, coagulate, though when separate show no such tendency, has led many to infer that the production of fibrin is rather due to the union of substances in the blood than to the decomposition of the same, as just explained. Indeed, according to Schmidt,[3] two such principles actually do exist in the blood, a fibrinoplastic substance, paraglobulin, and a fibrinogenous one, fibrinogen, whose union brought about by the presence of a ferment at the moment of coagulation constitutes fibrin.

Paraglobulin can be readily obtained from the serum of the blood through precipitation by the addition of sodium chloride in excess, and fibrinogen in the same way free from the liquor sanguinis, in which coagulation has been prevented by the addition of magnesium sulphate, and the corpuscles have been removed by filtration.

Now, while it is an interesting fact that if paraglobulin in a saline solution be added to either fibrinogen or hydrocele fluid, or if fibrinogen as obtained either from the liquor sanguinis or hydrocele fluid be added in saline solution to serum, fibrin will be produced, it does not necessarily follow that such a union as that of paraglobulin and fibrinogen actually takes place in the blood at the moment of coagulation. Indeed, it is yet to be proved that paraglobulin exists as such in the clot, seeing that if we obtain it from the serum it must be assumed that it exists in excess partly in the serum and partly in the clot. Again, as under certain circum-

[1] Annales des Sciences Naturelles (iv.), p. 25.

[2] Proc. of Glasgow Philos. Soc., 1845.

[3] Du Bois Reymond, Archiv, 1861, s. 545; 1862, s. 428. Pflüger's Archiv, 1872, s. 413; 1875, s. 291; 1876, s. 515.

stances, paraglobulin when mixed with fibrinogen does not produce fibrin, it is still further assumed that the presence of a ferment is necessary to effect the union of the two fibrin factors. As a matter of fact, an aqueous extract can be obtained from the serum by coagulating the latter with alcohol, allowing the mixture to stand, drying and pulverizing the clot, and then, adding water and filtering, which, when added to fibrinogen will cause the coagulation of the latter like a ferment. According to Schmidt, such a ferment is derived from the disintegration of the white corpuscles, the latter, as is well known, being always present in spontaneously coagulable fluids and very abundant if the coagulation is marked.

It was soon demonstrated, however, that the Schmidt theory of coagulation was untenable, Fredericq,[1] Hammarsten,[2] among others, proving that the clot was due to the coagulation of the fibrinogen in the presence of a ferment, the paraglobulin not entering into the formation of the clot at all.

It has been shown, however, in recent years, by Arthus and Pagès,[3] that if potassium or sodium oxalate be added to freshly drawn blood in sufficient quantities to precipitate its calcium salts, coagulation will be prevented, but that with the addition again of a soluble calcium salt coagulation will take place immediately. The Schmidt-Hammarsten theory has been, therefore, still further modified so as to take into account the influence exerted by the calcium salts in the production of coagulation. Thus, according to Pekelharing,[4] after the blood has been shed a fibrin ferment is formed through the union of a nucleo-albumin derived from leucocytes and blood plates with calcium. At the moment of coagulation the calcium leaves the nucleo-albumin and unites with the fibrinogen or part of it to form an insoluble calcium compound, fibrin. This view is based upon the fact that coagulation will take place if nucleo-albumin, together with calcium salts, be added to fibrinogen solutions, but will not take place if nucleo-albumin or calcium salts be added alone. A still more recent theory, that of Lilienfeld,[5] regards the fibrinogen as giving rise under the influence of leuconuclein to thrombosin, which combining with calcium forms the fibrin, the leuco-nuclein being derived from a proteid substance, nucleo-histon, obtained from the leucocytes and blood plates. It would appear, therefore, that the phenomena of coagulation is essentially that of the union of calcium with fibrinogen, through the influence of a third factor. Either a nucleo-albumin unites with calcium, and the latter then unites with fibrinogen, or a nucleo-albumin develops out of fibrinogen thrombosin, and the latter unites with calcium. It may be added that, according to these theories, blood

[1] Hoppe-Seyler: Physiologie Chemie, 1879, s. 416.
[2] Pflüger's Archiv, Band xix., s. 563.
[3] Archives de Physiologie Normal et Pathologique, 5 Série, Tome 2, 1890, p. 739.
[4] Untersuchungen über Das Fibrin ferment. Amsterdam, 1892, s. 15.
[5] Du Bois Reymond's Archiv für Physiologie, 1893, s. 560.

does not coagulate during life within the vessels, because the ferment being continually destroyed or changed does not exist at any one moment in sufficient quantity to produce this effect. When blood is shed, however, a relatively large amount of ferment being formed, coagulation takes place. Apart, however, from the insufficiency of the explanation, there still remains the fact entirely unaccounted for, that the blood under certain circumstances does coagulate during life within the vessels. Admitting that either or both of these theories be true, for they differ but little, it cannot be said that the cause of coagulation is explained. At best, they only establish what takes place during coagulation, not its cause.

CHAPTER XIII.

THE BLOOD.—(*Continued.*)

We have seen that the blood contains, either directly or indirectly, all the proximate principles of which the body is composed, including also the excrementitious matters, and that the food furnishes the materials out of which the vital fluid is elaborated.

As the composition of the blood must therefore vary in different individuals, and even in the same person from day to day and from hour to hour, anything more than an approximate analysis cannot be expected. The discrepancies as offered by the analyses of different chemists are due not only to this cause, but to the various methods made use of by them.

As the object of an analysis of the blood from a physiological point of view is to show not only the ultimate chemical elements entering into its composition, but the manner in which these exist in the blood, it will be readily understood that the investigation is an extremely difficult one.

While it is not necessary to describe in detail the analyses of the blood that have been made by different chemists, it seems proper that, at least, attention should be called to the general methods of investigation made use of at the present day.

During the last and preceding century a number of observations were made by which it was shown that the blood consisted of different principles. Thus Harvey discovered the proteid, Malpighi and Ruysch the fibrin, Guglielmini and Menghini some of the salts, Badia the iron, Rouelle the soda, etc.

Passing over these early and isolated observations,[1] it may be said that Macquer, a little more than a century ago, made the first analysis of the blood as a whole. With improved methods of chemical investigation the blood was more successfully analyzed by Berzelius in 1808. Some years later, 1823, Prevost and Dumas[2] published the results of their elaborate researches upon the constitution of the blood, and as their investigations have served as the starting-point for later analyses let us briefly review the method employed by these eminent chemists.

The blood to be analyzed is received into two equal vases, that of one vase is whipped so as to obtain the fibrin, which, when entirely separated, is weighed. The blood in the other vase is set aside to coagulate—that is, to separate into clot (fibrin and corpuscles) and serum (proteids, salts, water). The clot and serum are

[1] Milne Edwards, Physiologie, Tome i., p. 141.
[2] Ann. de Chemie et de Physique, 1823, Tome xxiii., p. 50.

then separated and desiccated so as to obtain the amount of water in them, and therefore in the blood of the second vase. As the clot consists of fibrin and corpuscles, if we subtract from the clot the fibrin obtained from the blood of the first vase, the remainder will give the quantity of the corpuscles in the blood of the second vase, or one-half the quantity in the whole blood examined. Having determined then the fibrin, water, and corpuscles, there remains the desiccated serum of the second vase to be analyzed for the proteids and the salts; the latter are determined by ordinary chemical analysis. Becquerel and Rodier determined the amount of proteids by treating the desiccated serum with boiling water, which separates the undetermined extractive matters and soluble salts, and then with alcohol, which dissolves the fats, the remainder being the proteids.[1] Figuier[2] suggested the improvement of estimating the corpuscles by adding to the defibrinated blood twice its volume of a solution of sodium sulphate and then filtering, the saline retaining them on the filter; any sodium sulphate that remains on the filter being removed by boiling water. Figuier's method of estimating the corpuscles can also be used as confirmatory of that of Dumas, the quantity of the corpuscles being estimated in their dry condition.

Composition of the Blood.

Water	781.600
Globules	135.000
Proteids	70.000
Fibrin	2.500
Serolin	0.025
Cholesterin	0.125
Sodium { Oleate, Margarate, Stearate }	1.400
Potassium, Sodium, Magnesium { Chloride }	3.500
Sodium, Potassium { Carbonate, Sulphate, Phosphate }; Free Soda; Magnesium { Sulphate, Phosphate }; Calcium phosphate	2.850
Iron	0.550
Extractives undetermined[3]	2.450
	1000.000

The general results of an analysis of the blood by such a method as that just given may be seen from that taken from Becquerel and Rodier's work, and which undoubtedly gives a very fair idea of the

[1] Traité de chimie de pathologique, p. 20. Paris, 1854.

[2] Ann. de Chemie, et de Phys., 1844, 3me serie, Tome xi., p. 506.

[3] Recent analyses have shown that these extractives consist of traces of dextrose, urea, lecithin, cholesterin.

average composition of the blood from a purely chemical, and, indeed, to a certain extent, from a physiological point of view also. It will be noticed at once, however, that in this analysis of 1000 parts of blood, there are present only 135 parts of corpuscles; whereas, anyone who is familiar with the appearance of living blood under the microscope knows that the corpuscles bear a much larger proportion to the plasma, the latter being to the corpuscles in the proportion of about two to one. This discrepancy is perfectly accounted for when we remember that, by the method of Becquerel and Rodier, the clot from which the corpuscles are estimated is dried and their water therefore driven off; the 135 parts of corpuscles represent, therefore, dry ones and not the living corpuscles, which, when united with their 370 parts of water, will amount to nearly 500 parts in the 1000 of blood analyzed.

Judging, also, from the boiled serum, we should expect to find a greater quantity of proteids than 70 parts per 1000 of blood. In the analysis just given the serum from which the albumin is determined is dried like the clot, hence the water present in living albumin is not given. When the water, however, is taken into consideration, the proteid will then amount to more than 300 parts in 1000 of blood. As the object of the physiologist is to ascertain if possible the quantity of proteids, fibrin, and corpuscles, as they exist in living blood, and as in this condition water is an indispensable element of their composition, it becomes a matter of importance to determine the quantity of these principles in a moist as well as in the dry condition. For these reasons Prof. Flint,[1] suggests that, while the fibrin be obtained in the usual manner of whipping—with broom-corn, for example—and the corpuscles by Figuier's filtering method, both these principles should be estimated in their moist condition, and not after desiccation; and that in determining the proteid from the serum, this should be treated as described above, but in the condition that it is found after coagulation—that is, with its water.

The difference between the results of an analysis of the blood by the method of Prof. Flint and that of MM. Becquerel and Rodier depends, therefore, upon the proteids, etc., being estimated, as combined with or without water, as shown by the following example:

Composition of the Blood

	Flint.	Becquerel and Rodier.	Difference is in water.	
Water	154.870	790.070	635.200	
Proteids	329.820	71.530	258.290	635.200
Fibrin	8.820	2.500	6.320	
Corpuscles	495.590	125.000	370.590	
Remaining matters, salts, etc.	10.900	10.900	00.000	
	1000.000	1000.000		

[1] Physiology, Vol. ii., p. 133.

We say the method of Becquerel and Rodier, not their actual analysis, for the quantities of proteids, fibrin, and corpuscles given under the method of Becquerel and Rodier, were experimentally obtained by Professor Flint by weighing the dry residue after desiccating these principles obtained by his method. It is very satisfactory, however, to see that the difference between the quantities of dry proteid and corpuscles given by Prof. Flint and Becquerel and Rodier are very slight, and that the quantity of fibrin is the same according to both. The remaining matters of the blood are determined in the same manner by these and other authorities by the ordinary methods of chemical analysis.

Of these, the larger proportion are the inorganic principles, and from a purely chemical point of view have been very satisfactorily determined, both quantitatively and qualitatively; but of the exact manner in which they exist in the living blood little is known beyond a few general statements to be noticed shortly.

The analyses of Prevost and Dumas, Andral and Gavarret, Lehmann, Becquerel and Rodier, Simon, Denis, Gorup Besanez, Schmidt, etc., while differing in detail, agree substantially in showing that the blood consists of water in molecular combination with or holding in solution albuminous substances, fats and sugars, and saline matters. It is interesting to observe in this connection that milk and eggs, the food of the young animal and embryo, consist of a mixture of water, proteids, fats, sugars, and salines, approximating closely in their composition to that of the blood; the value of such articles of food at all stages of life will be therefore readily understood.

We have seen that, under natural circumstances, the diet of man is a mixed one, and that beyond a limited period of time no single article of food, solid or liquid, will sustain life. As the blood is elaborated from the food it becomes impossible, therefore, to say positively that any one of its constituents is more indispensable to life than another. It is immaterial, therefore, with which we commence in describing their quantitative relations. We will follow, then, the order in which they present themselves in the analysis given by Becquerel and Rodier.

The absolute amount of water found in the blood, according to this analysis, amounts to 781.600 in the 1000; of this we have seen in life that over 600 parts enter into molecular combination with the proteids, fibrin, and corpuscles, forming an integral part of their composition. As the great use of water to the system has already been pointed out, it will not be necessary to dwell further on the importance of the large proportion in which it is present in the blood, merely stating that while the quantity varies within slight limits, any excess that may be taken in as food is rapidly eliminated by the skin, kidneys, etc., and that a deficiency in any amount materially alters the character of the blood.

Although water forms three-fourths of the blood, and however

indispensable it may be to health, yet the researches of Prevost and Dumas showed long since that there exists an intimate relation between the richness of the blood in organic matters and the vital activity of the organism.

Thus, while the quantity of water is large in all vertebrates, there is more water in the blood of the comparatively inactive fishes and batrachia than in birds and mammals, and that in those mammals which hibernate, implying a low order of vitality, the blood contains more water than in the ordinary members of this class. As regards the quantity of solid matters contained in the blood of vertebrates, the birds, whose vital activity is very high, come first, the mammals next, and finally the cold-blooded batrachia and fishes.

PROPORTION OF WATER, ETC., IN 1000 PARTS OF BLOOD OF VERTEBRATES.[1]

Animal.	Water.	Clot.	Proteid and salts.
Chicken	780	157	63
Pigeon	797	156	47
Duck	765	150	85
Raven	797	146	56
Heron	308	132	59
Monkey	776	146	78
Man	784	129	87
Guinea-pig	785	128	87
Dog	812	124	65
Cat	795	102	84
Goat	814	103	83
Calf	826	91	83
Rabbit	838	94	68
Horse	818	92	89
Sheep	836	86	77
Eel	846	94	60
Frog	884	69	46
Trout	864	64	72
Lota	886	48	66

It will be observed in the above that the corpuscles and fibrin are estimated together as clot. It should be mentioned, however, as showing the connection between the number of corpuscles and vital power, that it is the amount of corpuscles which varies in the different vertebrates, that of the fibrin being about the same. The amount of proteids, like that of the corpuscles, varies, but within much narrower limits.

Let us turn now to the consideration of the composition of the blood corpuscles and more particularly to their hæmoglobin. When blood is exposed, drop by drop to a cold of about −13.3° C. (8° F.) and then quickly warmed to 20° C. (68° F.), it will be observed that the corpuscles gradually lose their color, though they retain for a time their form and elasticity and that the serum becomes stained.

[1] Prevost et Dumas, Ann. de Phy. et Chim., 1823, T. 23, p. 64.

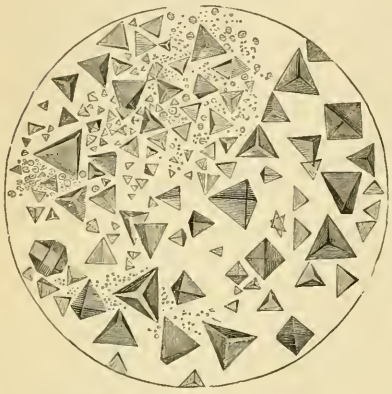
This is owing to the corpuscles consisting of a colorless protoplasmic material, the stroma to which their shape is due and of a coloring matter, the hæmoglobin. The latter constitutes about 94.3 per cent. of the solid matter of the corpuscles. It appears to exist according to Hoppe-Seyler[1] within the corpuscle in a state of combination the nature of which, however, is unknown. When hæmoglobin is set free as in the manner just mentioned and dissolves in the plasma, the blood not only changes its color but becomes transparent at least in their layers and is then said to be "laky." This condition of the blood can be brought about not only by alternate freezing and thawing but by the addition of bile, ether, chloroform, excess of water and by other means. It may be recalled in this connection that it is the sodium chloride of the blood existing in isotonic amount that prevents the blood corpuscles from absorbing water in excess, discharging their hæmoglobin and of so giving rise to a laky condition of the blood. According to Hoppe-Seyler the red corpuscles consist chemically of hæmoglobin in combination with oxygen or oxyhæmoglobin (94.3 per cent.), proteid, together with nuclein (5.1 per cent.), and of lecithin and cholesterin in traces (0.7 per cent.). Just as we have seen that the red corpuscle consists of stroma and hæmoglobin so it can be shown by appropriate means that the hæmoglobin consists of globulin and hæmochromogen. It is to the peculiar chemical constitution, however, of the latter substance that the hæmoglobin owes its spectrum and the readiness with which it combines with oxygen. Inasmuch, however, as hæmochromogen through oxidation becomes at once hæmatin it may be said that hæmoglobin practically consists of globulin, a proteid, and hæmatin, a pigment, the latter containing the iron of the blood, the globulin constituting 96 per cent., the hæmatin 4 per cent. Such being the case the red corpuscles will consist of stroma 5 per cent., of globulin 90.5 per cent. ($94.3 \times .96 = 90.5$), of hæmatin 3.8 per cent. ($94.3 \times 0.4 = 3.8$).

The coloring matter of the red corpuscles, the hæmoglobin, can be readily obtained in the form of crystals in several ways. Among other methods that might be mentioned, that of Preyer,[2] is as follows: Add enough water to a small quantity of defibrinated blood to make a clear solution and evaporate under a thin cover glass in a cool place. Should this plan fail add a little alcohol solution and place it in a freezing mixture. Usually crystals will at once form. These crystals are more readily obtained from some animals than others—with greater facility, for example, from the blood of the dog, horse, and guinea-pig, than from that of man, and only with difficulty from that of the bat, mole, and mouse. The form of these blood crystals varies also in different animals. Thus they are prismatic in form in man (Fig. 74), tetrahedral in the guinea-pig (Fig. 75), hexagonal in the squirrel (Fig. 76).

[1] Zeitschrift für physiologische Chemie, Band xiii., 1889, s. 477.
[2] Preyer, Die Blutcrystalle. Jena, 1871, s. 18.

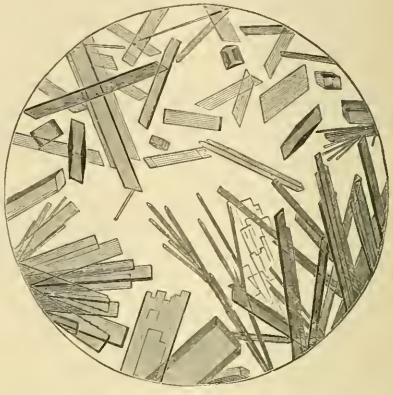
From whatever source they are obtained they are transparent and doubly refracting, and when oxygenated exhibit the color of the blood from which they were obtained. When deoxidized, however,

Fig. 74.



Prismatic crystals from blood of man.

Fig. 75.



Tetrahedral crystals from blood of guinea-pig.

they alternate in color from red to purple or green. They are soluble in water, alkalies, and most acids; insoluble in alcohol, and will remain unchanged for some time in urine, bile.

It is an interesting fact that although hæmoglobin crystallizes it does not dialyze readily, resembling in this respect colloidal bodies.

Fig. 76.

Hexagonal crystals from blood of squirrel.

Oxyhæmoglobin from the dog consists chemically, according to Hoppe-Seyler,[1] of C 53.85, H 7.32, N 16.17, O 21.84, S 0.39, Fe 0.43.

The exact molecular formula of hæmoglobin has not yet been established. If, however, the formula $C_{636}H_{1025}N_{164}FeS_3O_{181}$, as estimated by Hüfner[2] for dogs' hæmoglobin, be accepted as correct, the molecular weight will be 14001, and therefore very great. The amount of hæmoglobin present in a given quantity of blood can be determined from the amount of iron by colorometric methods and by the spectroscope. The iron method is based upon the fact that dry (100° C.) hæmoglobin contains 0.42 per cent. of iron. Knowing the amount of the latter in the blood the

[1] Med. Chem. Unters., s. 370.
[2] Hammarsten, op. cit., p. 69.

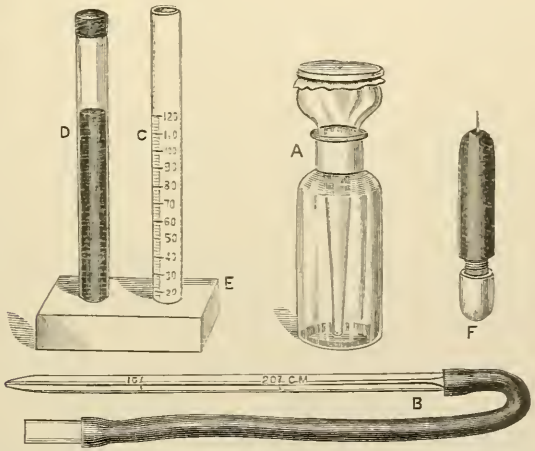
amount of hæmoglobin can be at once calculated by the following equation :

$$100 : 0.42 :: x : \text{Fe}, \; x \text{ equals } \frac{100 \text{ Fe}}{0.42},$$

in which x is the unknown quantity of hæmoglobin, Fe the known quantity of iron in the blood, and 0.42 the per cent. of iron in 100 parts of hæmoglobin. To obtain the amount of iron in the blood whose hæmoglobin is to be determined, a known quantity of blood is calcined, the ash is then treated with hydrochloric acid to obtain ferric chloride, which is then transformed into ferrous chloride by boiling with zinc until the liquid is colorless. The liquid being diluted, the amount of iron in it is determined volumetrically[1] by adding from a burette permanganate of potassium in standard solution until the rose color becomes permanent after agitation, 0.0056 gramme of iron being present for each centimeter of standard solution used. The hæmoglobin, as determined from the quantity of iron, amounts, according to Preyer,[2] in human blood to about 12.34 per cent.

The colorometric method depends upon the comparison of the tint of the blood to be investigated with that of a standard solution. In determining the amount of hæmoglobin in this way we make use of the hæmoglobinometer of Gowers. This consists (Fig.

FIG. 77.



A. Pipette bottle for distilled water. B. Capillary pipette. C. Graduated tube. D. Tube with standard dilution. F. Lancet for pricking the finger.

77) of two glass tubes (D and C) of exactly the same size. Into D are placed 20 cubic mm. of blood diluted with 2000 mm. of water; the strength of the solution is therefore 1 per cent. C is graduated, the scale of 100 degrees extending over a space equal to

[1] Sutton, Volumetric Analysis, 4th ed., pp. 88, 94. [2] Op. cit., s. 117.

that in D containing the 1 per cent. diluted blood. The manner of using the apparatus is as follows: Into C are placed 20 cubic mm. of the blood to be examined, which is then diluted until its color is the same as that in D. Suppose, for example, that we have to add to the blood to be investigated placed in C only 30 degrees of water (600 mm.) in order to obtain the same tint of color as that in D, instead of as in the latter case 100 degrees of water (2000 mm.), it follows that the blood in C contains only 30 per cent. of the normal quantity of hæmoglobin. Further, if the number of corpuscles in the investigated blood has also been shown to be only 60 per cent. of the normal amount, we have a fraction $\frac{30}{60} = \frac{1}{2}$, the numerator being the per cent. of the hæmoglobin and the denominator the per cent. of corpuscles, giving the average value of each corpuscle, or half the normal amount.

A still more delicate method of determining the amount of hæmoglobin is by spectrum analysis. This method is based upon the fact as shown by Preyer[1] that the red, yellow, and first bands of the green of the spectrum can be seen through an 0.8 per cent. solution of hæmoglobin and that such a solution can be taken as a standard of comparison. A known amount of the blood whose hæmoglobin is to be determined is, therefore, diluted until the same bands are seen with the spectroscope as with the standard solution. That being accomplished, the amount of hæmoglobin can be determined by the following equation:

$$x : k :: b + c : b$$
$$xb = k(b + c)$$
$$x = k\frac{(b + c)}{b}$$

in which

x = unknown quantity of hæmoglobin.
k = per cent. of hæmoglobin in solution (0.8).
b = volume of blood.
c = volume of distilled water.

Thus suppose, for example, that 2 c.c. of blood required 30 c.c. of water to give an absorption spectrum similar to that of the standard spectrum, the percentage of which is 0.8; then

$$x = 0.8\frac{(2 + 30)}{2} = 12.8 \text{ per cent. of oxyhæmoglobin.}$$

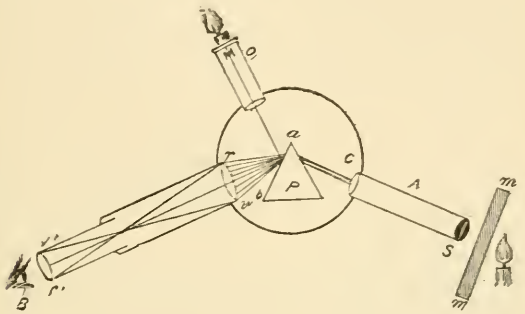
To appreciate the manner in which spectrum analysis is applied in the determination of hæmoglobin, or in the study of the blood generally, let us endeavor to explain briefly the principles of this method of investigation.

As is well known, when sunlight is transmitted through a prism, as in Fig. 78, it is decomposed into the seven colors, violet, indigo, blue, green, yellow, orange, and red. This is called the solar spectrum. In the early part of this century Fraunhofer described cer-

[1] Op. cit., s. 124.

tain lines situated in these colors, and which since then have been known as Fraunhofer's lines (Fig. 79, 7), and which in all probability are due to the presence of certain chemical elements existing in the form of vapor around the sun and which prevent the passage of certain rays emitted by the solar nucleus, it having been demonstrated that a vapor absorbs rays of light having the same

FIG. 78.



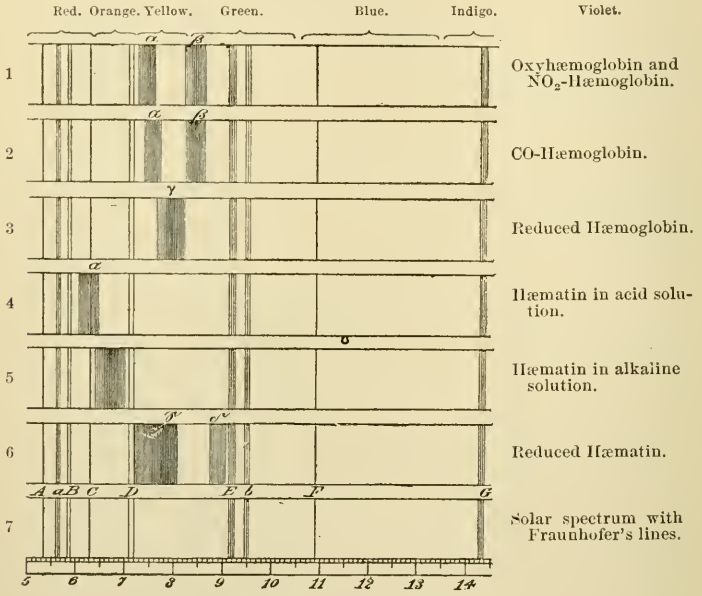
Scheme of a spectroscope for observing the spectrum of blood. A. Tube. S. Slit. *m m*. Layer of blood with flame in front of it. P. Prism. M. Scale. B. Eye of observer looking through a telescope. *r r*. Spectrum.

refrangibility as that which it emits. Thus a bright yellow line in the spectrum, due to incandescent sodium, will be replaced by a dark one if the light from the burning metal be intercepted by the vapor of the same. Since then it has been shown by Brewster, Herschell, and Müller that various colored solutions prevent the passage of certain of the rays of light, dark bands appearing in the spectrum in the place of the rays or colors arrested. In the same manner the influence of blood upon the passage of light through it was investigated spectroscopically (Fig. 78), more particularly by Hoppe-Seyler,[1] Stokes,[2] and Sorby,[3] and it was shown by these observers that when dilute arterial blood is used two dark bands appear (Fig. 79, 1) between the Fraunhofer lines *D* and *E*—that is, in the yellow of the spectrum, whereas if venous blood is used only one dark band (Fig. 79, 3) appears in the yellow near the line *D*. Further, it was demonstrated that this difference between arterial and venous blood was solely due to whether the coloring matter or the hæmoglobin was oxygenated or not, and that the fact of the arterial blood being red or scarlet, and of venous blood being blue or purple, was owing to oxyhæmoglobin being of a red hue and hæmoglobin of a bluish one. That the difference between arterial and venous blood spectroscopically, and as regards color, is due simply to the hæmoglobin being oxygenated in the former case and

[1] Virchow's Archiv, 1862, Band xxiii., s. 446.
[2] Proc. of Royal Society London, 1863, 1864, Vol. xiii., p. 355.
[3] Quarterly Journal of Science, 1865, Vol. ii., p. 198.

unoxygenated in the latter, can be readily demonstrated. Thus, if some reducing agent like ammonium sulphide or an alkaline solution of ferrous sulphate, kept from precipitation by tartaric acid, be added to arterial blood or the washings from a blood clot, the oxygen, being loosely combined with hæmoglobin, is at once seized with avidity by the reducing agent, the two dark absorption bands disappear, being replaced by the one dark band characteristic of venous blood, and the color changes from red to blue. On the other hand, with the exposure of venous blood or a solution of hæmoglobin to oxygen, or air containing such, the one dark band will disappear, being replaced by the two dark bands so characteristic of arterial blood, and the color will change from blue to red again.

Fig. 79.

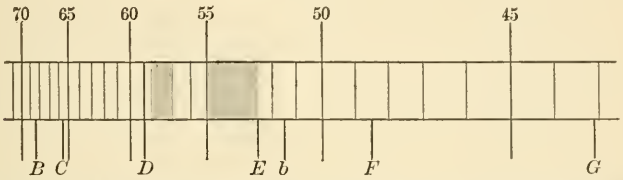


It will be observed as shown by Fig. 79, that the band situated toward the red end of the spectrum, often called the "α band," is narrower, darker and more defined than the band toward the green end, the "β band," the single band of venous blood being called the "γ band." It should be mentioned that the situation of these absorption bands is often described by stating the wave-lengths of those portions of the spectrum between which the bands are situated. Thus, for example, if the solution made use of in the investigation be one centimeter thick and contain 0.09 per cent. of oxyhæmoglobin, the "α band" is said to be situated (Fig. 80) between the wave-length $\lambda \frac{58}{100000}$ of a millimeter and $\lambda \frac{57}{100000}$ of a millimeter, the "β band" between $\lambda \frac{55}{100000}$ of a millimeter and $\lambda \frac{53}{100000}$ of a

millimeter. To make use of this method, however, the spectroscopes should be provided with a scale so disposed as to enable the observer to read off directly wave-lengths of any part of the spectrum.

According to the amount of oxyhæmoglobin present in the blood, or solution of oxyhæmoglobin used, the dark bands will vary in extent. Thus, in a concentrated solution the two bands run into one, there being a general absorption at the blue and red ends of the spectrum, also the light then passing through only the green and red parts. With a still further increase in the strength of the so-

FIG. 80.



Diagrammatic representation of spectrum of oxyhæmoglobin. The wave-lengths are indicated in hundred-thousandths of a millimeter by the numbers, the important Fraunhofer lines by the letters, the α band by the dark band to the right of D, the β band by that to the left of E. After ROLLETT, in Hermann, Band iv., s. 47, Fig. 5.

lution light will be transmitted through only the red portions of the spectrum, hence its red color, as seen by transmitted light. It is hardly necessary to add that the red rays are the last to disappear.

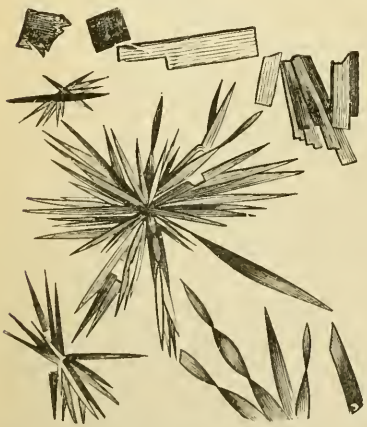
The extreme delicacy of spectrum analysis, as applied to the determination of the presence of blood, may be appreciated from the fact of the two bands appearing in the spectrum of light transmitted through a layer 1 centimeter thick of a solution containing only 1 gramme (15.4 grains) in 10,000 c. cm. (20 pints) of water, or, in round numbers, about 1 grain of hæmoglobin in a pint and a third of water. This is an important fact, since, under certain circumstances, in medico-legal cases, for example, the quantity of the suspected substance being exceedingly small, spectrum analysis would be the only means by which it could be determined whether it was blood or not. Indeed, substances already decomposed and putrid, solutions made by washing with water, old stains upon iron, wood, linen that may have lain aside unnoticed for years, can be shown by the spectroscope to contain hæmoglobin, and necessarily, therefore, to have been derived from blood, since no other known substance affects light as hæmoglobin.

Even if the spectrum obtained was that of carbon monoxide, or hæmoglobin (acid hæmatin), characterized by two and one absorption bands respectively (Fig. 79, 2, 4), as in the case of arterial and venous blood, this need be no source of confusion, since the absorption bands of these substances are not situated in exactly the same part of the spectrum as those of arterial and venous blood, and even if a doubt existed as to the exact locality of the bands, there could be none with reference to the presence of

blood, as it is the hæmoglobin in each case which is the cause of the appearing of the bands. It should be mentioned in this connection that spectrum analysis, like all other means at present at our command, enables us only to determine that a substance is blood, but not necessarily human blood. In examining the blood spectroscopically, while the ordinary spectroscope can be used, the microspectroscope will be found more convenient, and especially the form described by Vierordt.[1]

It may be mentioned here as well as elsewhere that there are several other compounds or derivatives of hæmoglobin, many of which have a characteristic spectrum and are of more or less interest as well as that of oxyhæmoglobin. Thus, for example, there are substances: methœmoglobin, differing only from oxyhæmoglobin in that its oxygen is more stable; hæmochromogen derived from the decomposition of hæmoglobin in the absence of oxygen; hæmatin on the contrary in the presence of the latter; hæmotoidin obtained from the hæmoglobin of extravasations such as apoplectic clots, corpora lutea, etc. Histio-hæmatins, pigments found in the tissue and supposed to be derivative of hæmoglobin, of which myohæmatin already referred to is an example. Hæmatoporphyrin or iron-free hæmatin obtained through the action of sulphuric acid upon hæmatin. Hæmin through the action of hydrochloric acid upon the same. Hæmin being of especial interest from a medico-legal point of view, its chemical composition, and principal properties and method of obtaining will be briefly noticed. Hæmin as shown by its chemical composition ($C_{34}H_{35}N_4O_5HCl$) is a hæmatin hydrochlorate and can be obtained by the addition of hydrochloric acid to hæmoglobin, 100 parts of the latter yielding about 4 parts of hæmin. Hæmin is insoluble in alcohol and water, but soluble in acids and alkalies, and can be obtained from a very minute portion of blood by the following method: Triturate the suspected substance with a little common salt and add glacial acetic acid, then warm the mixture till bubbles appear, and then cool it. If the substance, thus treated, contain hæmin, the latter will appear (Fig. 81) as crystals, in the form of rhombic tablets disposed sometimes as stars or crosses of a red or brown color. If oxygen be added, the color of the crys-

Fig. 81.



Rhombic crystals of hæmin or hydrochlorate of hæmatin.

[1] Die Quantitative Spectral Analyse in ihrer Anwendung auf Physiologie. Tübingen, 1876.

tals assumes a violet hue, while under the influence of carbon dioxide the crystals lose their transparency. In medico-legal questions where there may be a very small quantity of material to be examined, the presence of hæmin crystals will settle the question as to whether the suspected material is or is not blood. Hence, the importance of the method just given from this point of view. It should be mentioned, however, that the obtaining of hæmin as well as of hæmoglobin crystals by whatever method only proves that the material from which they were extracted was blood, but not necessarily human blood.

In the fact of the oxygen of the blood existing, for the most part, in a state of loose chemical combination with the hæmoglobin lies the explanation of the manner in which blood absorbs or gives off oxygen. Did the oxygen exist simply in a state of solution in the blood then the amount absorbed, or given off, would depend upon the amount of pressure present. That such is not the case, however, can be shown by exposing venous blood, containing little or no oxygen, to a succession of atmospheres containing increasing quantities of oxygen. At first there is a very rapid absorption of oxygen, but afterward this diminishes or ceases altogether. On the other hand, if arterial blood, containing a considerable quantity of oxygen, be exposed to successively diminishing pressures, at first little oxygen is given off, but afterward the escape is sudden and rapid. The amount of oxygen taken up or given off by blood is not, therefore, dependent upon pressure, except so far as the latter influences the passage to or from the plasma, but upon chemical affinity; the oxygen absorbed or given up by the hæmoglobin is therefore a constant quantity. The amount of oxygen absorbed by dogs' hæmoglobin, for example, is 1.59 c. cm. per gramme, the temperature being 0° C. and the barometric pressure 760 mm.,[1] one molecule of hæmoglobin absorbing one molecule of oxygen. It is generally supposed that the property of absorbing oxygen exhibited by hæmoglobin depends upon the iron that it contains, one molecule of oxygen being taken up for each atom of iron in the molecule of hæmoglobin. The amount of oxygen that will be absorbed by the blood in any instance can therein be estimated from the amount of iron as well as from the hæmoglobin present. It may not be inappropriate to mention that the oxygen absorbed, or given off by the hæmoglobin, has nothing to do with the oxygen entering into its molecular composition, and as already given in its chemical formula.

That the hæmoglobin is that part of the blood which absorbs and gives up the greatest part of the oxygen there can be no doubt, since, if serum freed of the corpuscles, and therefore of hæmoglobin, (the latter constituting 90 per cent. of the former), be experimented with instead of blood, little or no oxygen is absorbed, or given off, perhaps $\frac{1}{2}$ per cent. of the entire blood, of which the serum was a

[1] Hüfner, Zeits. für phys. Chemie, Band ii., 1877–78, s. 389.

part, and that proportional to the pressure. It is, therefore, to their hæmoglobin that the red corpuscles owe their function, as we have seen, of being oxygen carriers and, since the hæmoglobin at low pressure readily gives up its oxygen, the functional significance of this substance, in respiration, becomes very evident.

It may be mentioned in this connection that the carbon dioxide present in the blood is not simply dissolved there, but exists principally in the form of sodium carbonate and bicarbonate since the absorption and giving up of carbon dioxide by the blood is not dependent upon pressure. It is generally held that these salts are decomposed and the carbon dioxide set free by the hæmoglobin of the red blood corpuscles, the latter being supposed to act as an acid. That such is the case, is shown by the fact that more carbon dioxide can be obtained from blood than from serum, and that after all the carbon dioxide has been extracted from the serum that is possible by the gas pump, two to five per cent. more can be obtained by adding acid. It is quite possible that the acid action of the hæmoglobin, just referred to, may be aided to some extent by the serum-albumin and primary acid phosphate of the blood.

According to the recent investigations of Bohr,[1] however, it appears that if hæmoglobin be exposed to a mixture of oxygen and carbon dioxide, it will absorb carbon dioxide as well as oxygen, the former combining possibly with the globulin and the latter with the hæmochromogen. If such be the case hæmoglobin must be regarded to some extent at least as a carrier of carbon dioxide as well as aiding in the decomposition of the alkaline carbonates and of so setting free carbon dioxide.

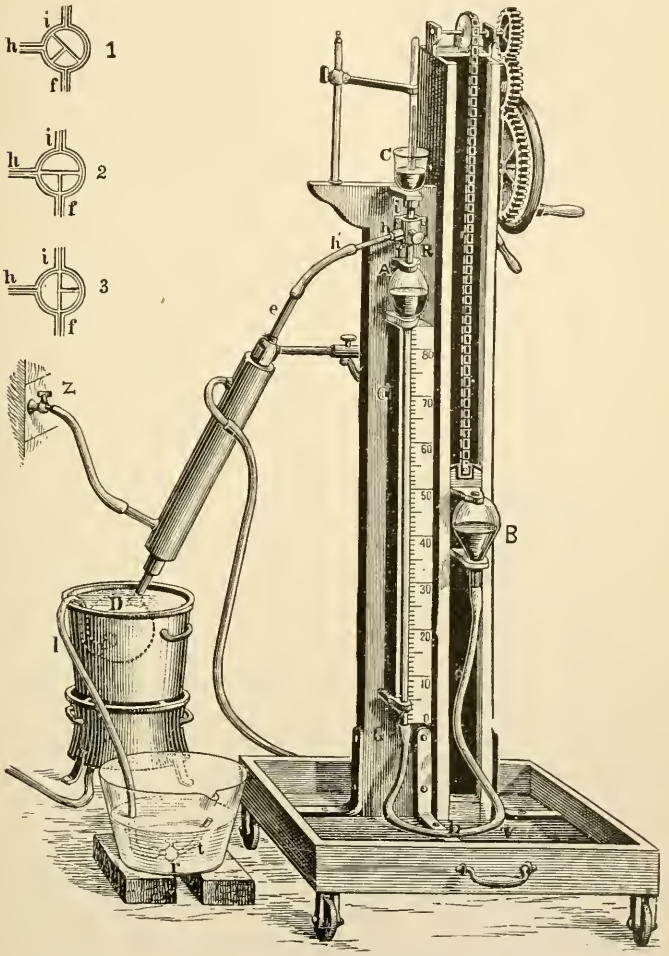
The small amount of nitrogen that the blood contains appears to exist there in a simple state of solution, the blood absorbing but little less nitrogen than that absorbed by water; the amount depending, at least, within limits upon the law of pressure.

The gases of the blood, as has just been incidentally mentioned, can be obtained by subjecting the blood to the mercurial vacuum. For this purpose we make use of Grehant's gas pump. This consists (Fig. 82) of a glass reservoir (B), which can be lowered or raised by a rack and pinion, and which communicates by the flexible tube b with the vertical glass tube c, which is firmly secured to the stand. The vertical tube expands into the oval-shaped dilatation A, which is continued upward as the narrow tube f, and whose cavity by means of the stopcock R, can be put in communication either with that of the lateral tube h, or of the tube i terminating above in the cup C, or cut off from either. The lateral tube h is connected through tubing (h′) with the stem e of the bulb D, into which is inserted a flexible tube (l) furnished with a stopcock (r), for the transference of the blood whose gases are to be determined. The stopcock (R) being in the position 1, Fig. 82—that is, all communication between the cavity of the vertical tube c

[1] Skandinavisches Archiv für Physiologie, Leipzig, 1891, Band 3, s. 47.

being completely cut off from that of the lateral and terminal tubes h and i, mercury is poured through the reservoir B until it not only rises to the level of the stopcock, but completely fills the reservoir itself. The reservoir being then lowered the mercury will fall in the vertical tube c, a vacuum being produced in consequence

Fig. 82.

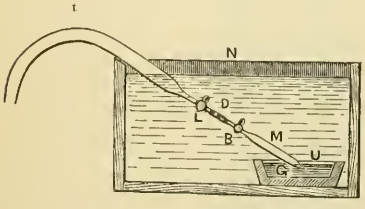


Grehant-Alvergniat gas pump.

above it. If the stopcock be now turned into the position 2 (Fig. 82), the air will pass in from the lateral tube and its appendage into the vertical tube c, and the mercury will fall still lower. The stopcock being now returned into the position 1 (Fig. 82), the reservoir is then elevated, and the mercury with the included air

will ascend into the oval dilatation A. The stopcock being now turned into the position 3 (Fig. 82), the air that was just drawn into the vertical tube c from the lateral tube h passes out of the tube i into the atmosphere. The stopcock is then returned to the original position (Fig. 82, 1). By depressing and elevating the reservoir B, and manipulating the stopcock R in the manner just explained, in a very short time a good vacuum is produced in the lateral tube h h′ e, and its appendage D. A tube having been inserted into the artery or vein, the blood to be analyzed is then transferred from the vessel in the living animal to the vacuum in the following manner: A tube (M) of known capacity, say 50 c.c., tapering off at one end (G), and guarded by a stopcock (B) at the other, is filled with mercury by aspiration. The tube is then at the end G put in communication with the blood vessel, by means of a rubber tube readily slipping over the canula previously inserted into the vessel, which is closed by a clip. The stopcock being now opened, and the clip removed, the blood is allowed to flow away for a moment, and then (connection being made by the tubing) into the tube M, driving out of the latter the mercury, which can be received into a convenient receptacle. As soon as the tube is filled with blood, the stopcock being closed, connection is broken with the vessel, and the tube reversed in position, so that its tapering end G (Fig. 83) may be inserted into the small mercury trough U, previously placed in the large trough N containing ice-water, to retard the coagulation of the blood in the tube. The glass tube is then joined by the end B to the rubber tube D provided with a stopcock (e) containing boiled distilled water, and previously placed over the tube t (Figs. 82, 83), the latter being furnished with a stopcock (Fig. 82, r) and leading to the vacuum. Both stopcocks (B and r) being now opened, the blood passes from the glass tube (Fig. 83, M) into the vacuum D e (Fig. 82), its place being filled with mercury from the trough; the stopcocks are then closed. The blood having passed through the tube in the bulb D, gives up its gases readily into the vacuum, the liberation of which is greatly facilitated by surrounding the bulb with water (Fig. 82) at a temperature of about 40° C. (104° F.). As it is also desirable to keep back the froth and foam arising from the blood as much as possible, the lateral tube e is surrounded by a tin one, through which ice-cold water flows from a reservoir (z), and which effectually accomplishes the object. The gases having been separated from the blood, are next transferred into the vertical tube c, and thence through the terminal one i into a eudiometer, standing over mercury in the cup C, by depressing the mercurial reservoir B, and

Fig. 83.



turning the stopcock R in the same manner as just explained. The quantity of blood from which the gases are obtained will, of course, depend upon the size of the tube transmitting the blood from the vessel to the vacuum, the vessel being clamped as soon as the tube is full of blood.

In order to determine the nature and amount of the gases given off from the blood we make use of an eudiometer in the usual way or of a Hempel's apparatus, which enables us to conveniently transfer the mixture of gases successively into a solution of caustic potash and pyrogallic acid, etc., and of so determining by absorption the amount of carbon dioxide and oxygen present, the gas remaining over being usually regarded as consisting of nitrogen. The volume of the gas obtained must be reduced, of course, to standard pressure 760 mm. mercury, and standard temperature 0° C., which can be done by the following formula: $V = \frac{V' \times (h - p)}{760\,(1 + at)}$ in which V is the required volume at standard temperature 0° C. and standard pressure 760 mm., V' the volume at the observed temperature and pressure, h the observed pressure, p the tension of the aqueous vapor, a the coefficient of expansion, a constant (.00366), and t the observed temperature.

The formula is derived as follows. Firstly, with reference to the correction of the given volume for temperature:

$$1 + at : 1 :: V' : V \text{ or } V = \frac{V'}{1 + at}.$$

And secondly, for pressure:

$$V : \frac{V'}{1 + at} :: (h - p) : 760 \text{ or } V = \frac{V' \times (h - p)}{760\,(1 + at)}.$$

As an illustration of the manner of using the formula, let us suppose that 30 c. cm. of nitrogen, or V', were collected at 15° C., 740 mm. barometric pressure, 12.677 mm. being the aqueous tension, then V, or the required volume, would be, at 0° C., and 760 barometric pressure, 27.23 c. cm.

$$V = \frac{30\,(740 - 12.677)}{760\,(1 + .00366 \times 15)} = \frac{30 \times 727.323}{760 \times 1.0549} = \frac{21819.690}{801724} = 27.23 \text{ c.cm.}$$

It will be found on an average that for 100 vol. of blood used there will be extracted by means of the mercurial pump about 60 vols. of gas, the barometric pressure being 760 mm. (30 cub. in.) and the temperature 0° C. (32° F.), and that the composition of this gas will be according to the kind of blood examined, as follows:

	Oxygen.	Carbon dioxide.	Nitrogen.
Arterial blood . .	20 vol.	39 vol.	1 to 2 vol.
Venous blood . .	8 to 12 "	46 "	1 to 2 "

The amount of oxygen accords with the fact already mentioned that 1 gramme of hæmoglobin combines with 1.59 c.c. of oxygen, since if it be admitted that 100 c.c. of blood contain 15 grammes of hæmoglobin, then 100 c.c. of blood should contain 23.85 vols. per cent. of oxygen, the excess of oxygen over that actually found being due to the fact that the hæmoglobin of the blood is not saturated.

The proteid material of the plasma of the blood consists of three substances, serum-albumin, paraglobulin, and fibrinogen. The principal properties and reactions of these three proteids having been already noticed, but little remains to be said of them in this connection. Owing to the property possessed by paraglobulin and fibrinogen of being precipitated when blood is saturated with magnesium sulphate ($MgSO_4$), a means is thereby offered of separating the serum-albumin from the other two proteids. Serum-albumin exists in human blood to an amount of 45.20 parts per thousand. Although the peptones and proteoses, or the digested proteid food, differs in many respects from serum-albumin, the latter must be derived in the long run from the proteid material of the food. The transformation of peptone, etc., appears to take place, however, not within the alimentary canal, but during absorption, as the peptone, etc., passes through the walls of the alimentary canal into the blood. Just as the proteid substances of the food are the sources of the serum-albumin of the blood, so the latter is the source of the proteid material of the tissues. It should be mentioned, however, that the tissues do not derive their supply of proteid material directly from the blood, but rather from the lymph by which the cells of the tissues are bathed. Paraglobulin exists in human blood to an amount of 31 parts per thousand. It has been stated that there is more paraglobulin in serum than in an equal amount of plasma, the excess of paraglobulin being accounted for on the supposition that it is derived from the substance of the leucocytes disintegrated during coagulation. However this may be, the fact of paraglobulin existing in such an amount in the plasma, renders it probable that, like serum-albumin, it is derived from nitrogenous food and is a considerable source of the proteid material of the tissues. Apart from these meagre statements, and what has been said elsewhere, nothing definite is known either as to the origin or uses of paraglobulin. Fibrinogen, the third proteid of the plasma, exists in human blood only in small amounts, from 2–4 parts per thousand. It differs in several respects, as already mentioned, from paraglobulin. Apart from the theory already referred of fibrinogen being the source of the fibrin of the blood, nothing is positively known as to its use in the economy, still less as to its origin.

The fatty matters that are found in the plasma consist of cholesterin, phosphorized fats, and saponified principles like the margarates, oleates, oleic acid existing sometimes in a free state. The fatty substances exist only in small quantities in the blood, and often depend upon the kind of diet. Thus fatty food increases the

amount of fat in the blood. The use of these fatty substances in the blood is not exactly understood.

The saline materials of the plasma consist of sodium, potassium, and magnesium chlorides, some free soda, of sodium and potassium carbonates, of sodium, potassium, and magnesium sulphates, of sodium, potassium, magnesium, and calcium phosphates; in a word, three chlorides, free soda, two carbonates, three sulphates, four phosphates. It is possible that these salts do not always exist in the blood in the above form, that arrangement being due perhaps to the difficult and complicated processes incidental to their analysis. It is well known that a considerable quantity of the earthy phosphates is molecularly united with the fibrin and part of the sodium chloride with the albumin. The natural relation of these salts as well as that of the others must, therefore, to a certain extent, at least, be disarranged in an analysis.

The importance of these salts is seen not only in the nutrition of the tissues, the calcium and magnesium phosphates, for example, supplying material for the production of bone, but they are also indispensable in maintaining the blood in its proper chemical and physical condition. Thus the alkalinity of the blood is due to its sodium carbonate, while the sodium phosphate dissolves the albuminous principles and inorganic matters which are insoluble in pure water. The earthy phosphates are held in solution in the serum through the presence of this salt, and to it is due the fact that so much carbon dioxide is dissolved in the blood.

The existence of the corpuscles depends on the presence of sodium chloride and other salts in the serum, which, existing in isotonic amounts absorb any superfluous water, and prevent their dissolution. According to Milne Edwards, the coloring matter of the corpuscles is very soluble in water, but not so in water to which have been added albumin and sodium chloride, both of which are found in the serum. While probable, yet it cannot be stated positively that age or sex influences the quantity of these salines. There is no doubt, however, that these principles vary in quantity according to the kind of food. An exclusively animal or vegetable diet will affect the amount of alkaline phosphates respectively. Thus the former are most abundant in the blood of the carnivora, the latter in that of the herbivora. The proportion of the saline principles of the blood is also known to vary in disease; but the limited data, however, that have been collected are of more interest at present to the pathologist than to the physiologist. One of the most important substances found in the blood is iron. Indeed, when it is deficient the red corpuscles diminish in number. The normal standard is soon regained, however, when iron is administered. The iron exists in the blood combined with the coloring matter of the corpuscles; the color of the latter, though, does not depend upon the iron, as was once supposed, for the color will remain after the iron is removed, while the blood of certain inverte-

brates like the Limulus (horseshoe crab) is colorless, though iron is present.

From the description of the blood just given, it will be seen to consist of water, corpuscles, proteids, inorganic salts, and extractives.

If the composition of the corpuscles be now compared with that of the liquor sanguinis, it will be found that the corpuscles contain the phosphorized fats, the liquor the fatty acids. The potash salts are confined almost entirely to the corpuscles, the soda salts to the liquor; the latter containing about four times as much soda as the former. All of the iron in the blood is contained in the corpuscles, the greater part of the earthy phosphates, on the contrary, in the liquor. The relative densities, quantity of water, solid matters, proportion of salts in the corpuscles, and liquor sanguinis, are given somewhat in detail in the following table:

BLOOD, IN 1000 PARTS EACH.[1]

	Corpuscles, 513.		Liquor sanguinis, 487.
Density	1.0885		1.028
Water	681.63		901.51
Solid matters	318.37		98.49
	1000.00		1000.00
Hæmatin	15.02	Fibrin	8.06
Globulin	296.07	Extractives	81.92
Inorganic salts	7.28		8.51
	318.37		98.49
Sodium chloride	....		5.546
Potassium chloride	3.679		0.359
Potassium phosphate	2.343		....
Potassium sulphate	0.132		0.281
Sodium phosphate	0.633		0.271
Soda	0.341		1.532
Calcium phosphate	0.094		0.298
Magnesium phosphate	0.060		0.218
Iron	undetermined		....
	7.281		8.505

In concluding our account of the blood a few words may be said in reference to transfusion, though this subject is usually considered as belonging to therapeutics. About the middle of the seventeenth century experiments were performed which showed that life could be saved in an animal dying from a copious hemorrhage, for example, by introducing into its vessels fresh blood from an animal of the same species. Application was soon made of this fact in the treatment of human beings, and the wildest enthusiasm was excited, great hopes being entertained that old age could be rejuvenated, etc. Several fatal cases of transfusion, however, occurring, the practice was prohibited in many places by law. It was revived in the early part of this century, and with success. There being a

[1] Schmidt, in Ranke Physiologie, s. 350. Leipzig, 1875.

number of cases on record [1] which would have undoubtedly proved fatal had not transfusion been used.

In recent years, however, it has been shown in the case of certain animals, at least the dog and rabbit, for example, that if the serum of the former be introduced into the blood of the latter animal, its blood corpuscles will be disintegrated and the blood rendered laky. This deleterious effect of the serum, together with intravascular clotting, due to the introduction of fibrin ferment, have been assigned as causes of the mortality following transfusion and used as arguments for the discontinuance again of the practice. It has been recommended, therefore, in cases of severe hemorrhage, demanding transfusion, that an isotonic solution of sodium chloride (0.6 per cent.) be introduced instead of blood or serum, which will not injure the corpuscles, but by increasing the bulk and velocity of the circulating fluid and preventing stagnation, will make them more efficacious as oxygen carriers.

Having studied the composition and properties of the blood generally, let us now turn to the consideration of its circulation.

[1] Berard, Physiologie, Tome iii., p. 219. Paris, 1851.

CHAPTER XIV.

CIRCULATION OF THE BLOOD.

The Heart.

We have seen that the use of the food is to repair the waste of the tissues, to supply fuel for the production of energy, and that the food is digested, absorbed and gradually elaborated into blood. To supply the wants of the system, to furnish the tissues with material for their maintenance and repair, to carry away that which has become worn out and effete, the blood must move freely through all parts of the economy. It must circulate. By the circulation of the blood is meant that the blood moves in a circle—that is, if we follow its course, for example (Fig. 84), after it passes from the left ventricle of the heart to the aorta we shall see that the blood flows from the aorta into the arteries, thence into the capillaries, from there into the veins, from the latter by the vena cava into the right side of the heart, from the right side of the heart through the lungs back to the left side of the heart to the left ventricle, where it started.

Usually the passage of the blood from the right auricle of the heart through the lungs and left ventricle is known as the lesser, or pulmonary circulation, while the route from the left ventricle through the arteries, capillaries, and veins to the right auricle is distinguished as the greater or systemic circulation. Using the word circulation in the sense in which it is ordinarily accepted, the terms lesser and greater circulations are not appropriate, and may mislead, inasmuch as we have seen that the blood does not pass directly back from the lungs to the right auricle of the heart, whence it came, but indirectly, first coursing through the system, and that the blood flowing from the left ventricle only returns there after having passed through the lungs. There is, in this sense, then, only one circulation, however conveniently the latter may be divided into the so-called lesser and greater circulations. In another sense, however, there are innumerable circulations, greater and lesser, since the blood, after leaving the heart (Fig. 84), may go either to the head, or viscera, or extremities before returning to the heart.

As the motion of the blood is in a circle, it is immaterial at what part of the vascular system we begin its study. We shall see, however, that in exposing any of the great functions of the body, if we follow, as far as practicable, the order in which the facts were actually discovered, and the phenomena generalized by the human mind, that the subject will be presented in the most natural logical

sequence. We will begin, therefore, the study of the circulation of the blood, with the demonstration of the structure and function of the heart.

FIG. 84.

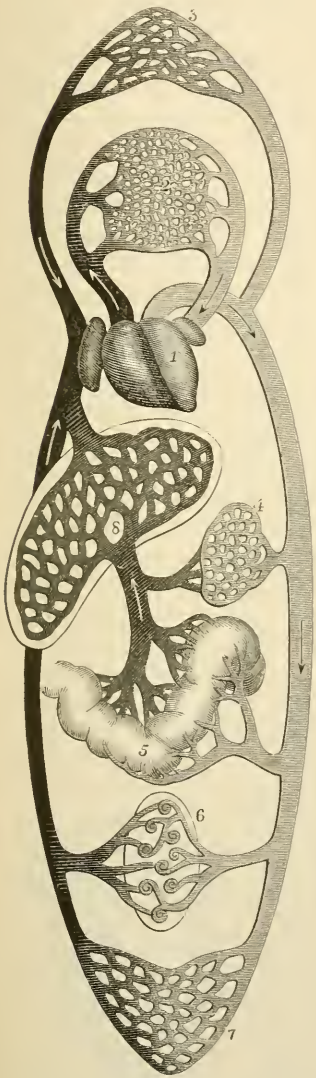
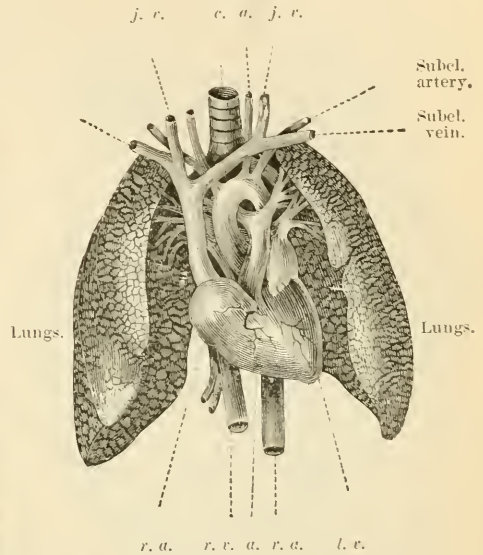


Diagram of the circulation. 1. Heart. 2. Lungs. 3. Head and upper extremities. 4. Spleen. 5. Intestine. 6. Kidney. 7. Lower extremities. 8. Liver. (DALTON.)

FIG. 85.



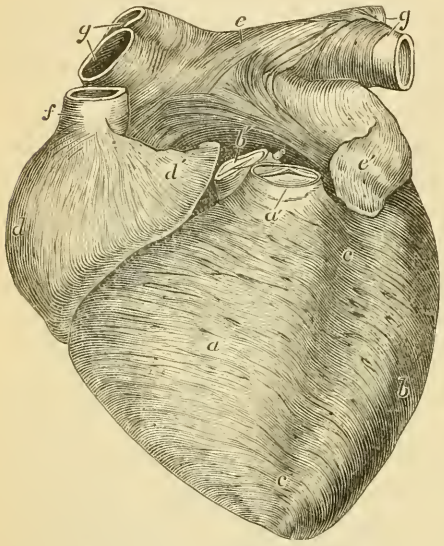
Heart and lungs of man. (MILNE EDWARDS.)

The heart is a hollow pear-shaped muscular organ. It is situated in the thoracic cavity, and lies between the lungs, with which it is connected by the great blood vessels arising from its base (Fig. 85). The heart is loosely enclosed in a sac, the pericardium. This sac, having the form of the heart, and of a bluish-white color, consists of two layers. The external fibrous layer, continuous with the external coat of the great blood vessels, consists of fibrous tissue, and is a strong, inextensible membrane. The internal delicate serous layer does not differ essentially in its general character from that of serous membrane. It surrounds the heart closely adhering to it and is then reflected over the commencement of the great blood vessels and the interior surface of the external fibrous membrane. The cavity of the pericardium contains about a drachm or two of a serous fluid, through the presence of which the opposed internal surfaces of the

pericardium glide smoothly over each other, the movements of the heart being thereby facilitated.

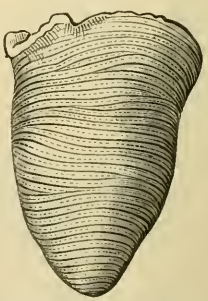
The pericardium is attached by connective tissue to the pleura on each side, and the tendinous center of the diaphragm below. It is not necessary to give a detailed, minute description of the disposition of the muscular fibers of the heart, which is quite complex, a general account in connection with the present subject being sufficient. The auricles, or upper cavities of the heart (Fig. 86, *d*, *e*), are encircled by a thin layer of muscular fibers, common to both these cavities, and surrounding the auricular appendages, the entrance of the vena cava, the coronary and pulmonary veins. Beneath this superficial layer are the fibers of the deep layer attached to the fibrous rings of the auriculo-ventricular orifices, and disposed in an annular and loop-like manner. The muscular fibers of the ventricles, like those of the auricles, are also arranged in two sets, superficial and deep. The superficial fibers (Fig. 86, *a*, *b*), which are common to both ventricles, run from base to apex, and at this point pass into the interior of the ventricle in the form of a whorl or spiral, some of the fibers terminating in the columnæ carneæ and papillary muscles, others returning after a twisting course to the point from which they started. The fibers of the deep set (Fig. 87) surround each ventricle separately, and are disposed in a circular or transverse manner between the external and internal layers of the superficial fibers, and are much better developed in the left ventricle than in the right.

Fig. 86.



Anterior view of heart. (Quain.)

Fig. 87.



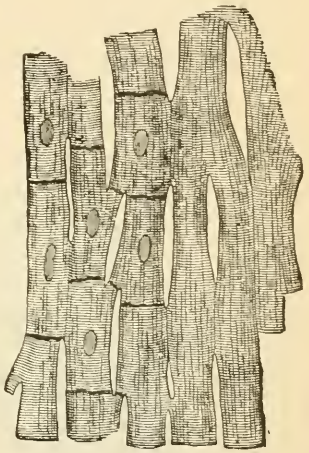
Left ventricle of bullock's heart, showing the deep fibers. (Dalton.)

Microscopically the muscular substance of the heart consists of transverse striated muscular fibers. These fibers, however, differ from the ordinary fibers of voluntary muscles in several particulars. They are destitute of sarcolemma, much smaller and more granular, not collected into bundles, and are separated by comparatively little connective tissue. The most in-

teresting peculiarity, however, about these fibers, is their anastomosing or inosculation with each other (Fig. 88), which, no doubt, favor the contraction of the heart and the thorough expulsion of the blood from its cavities.

If a longitudinal section be carried through the heart from base to apex, its interior will be seen from such a section to consist of four cavities: two auricles, so called from their auricular appendages, and two ventricles; that the right auricle communicates with the venæ cavæ and with the right ventricle, and the left auricle with the pulmonary veins and the left ventricle; there is no communication, however, between the two auricles or between the two ventricles; the right or venous side of the heart being completely separated from the left or arterial side by the septum of the heart, which is imperforate.

Fig. 88.



Muscular fibers of the heart. (Quain.)

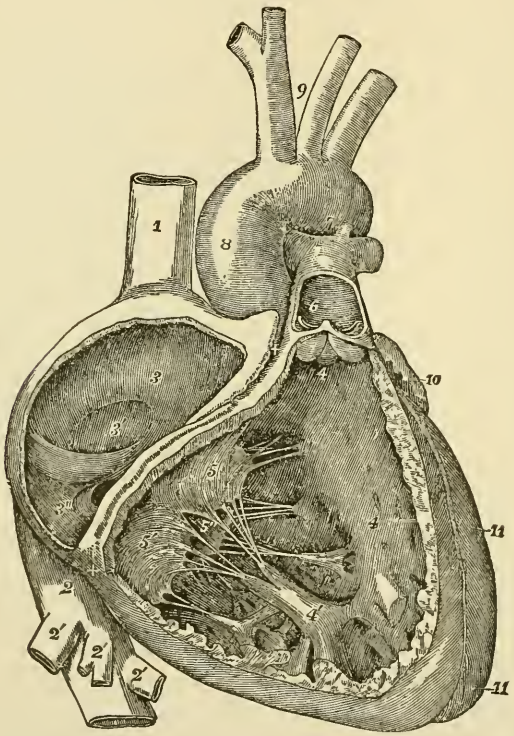
In certain mammals, in the dugong (Halicore) and manatee (Manatus) for instance, this distinction of the right from the left side of the heart is to a certain extent visible, even externally, the ventricles at the apex being separated by quite an interval.

We have just seen that the heart is covered with the serous layer of the pericardium. It will be observed that the interior of the heart is also lined by a thin translucent membrane, the endocardium, which is continuous with the internal coat of the blood vessels and consists of a fibrous elastic and epithelial layer. Just at the point where the auricles pass into the ventricles, the endocardium projects into the cavity of the heart from the wall of the heart on one side, and from the septum on the other. This portion of the endocardium is strengthened by the addition of fibrous tissue. It is these projections that serve to divide the auricles from the ventricles. The interval left between these projections constitutes the auriculo-ventricular orifices. The fibro-elastic tissue in this situation forms a slight ring, to which is attached on the right side of the heart the tricuspid valve (Fig. 89, Fig. 91, 5, 5′, 5″), three membranous folds, which consist of doublings of the endocardium thickened by the included fibrous tissue. By means of these curtains or valves, the auriculo-ventricular orifice can be closed, the edges of the valves being then pressed together (Fig. 91), as we shall see, by the blood, and are kept stretched by the tendinous cords as the sail of a boat is kept stretched against the wind by the sheet line.

The chordæ tendineæ are tendinous cords inserted into the valve, and arise either directly from the walls of the ventricle or are con-

nected with it by the papillary muscles. Of these latter many pass directly again into the substance of the heart and are then known as the fleshy columns or columnæ carneæ. During the repose of the ventricle the auriculo-ventricular orifice is open, the valves then lying loosely against the walls of the ventricle. The same disposition, such as we have just described, obtains essentially in the left

FIG. 89.



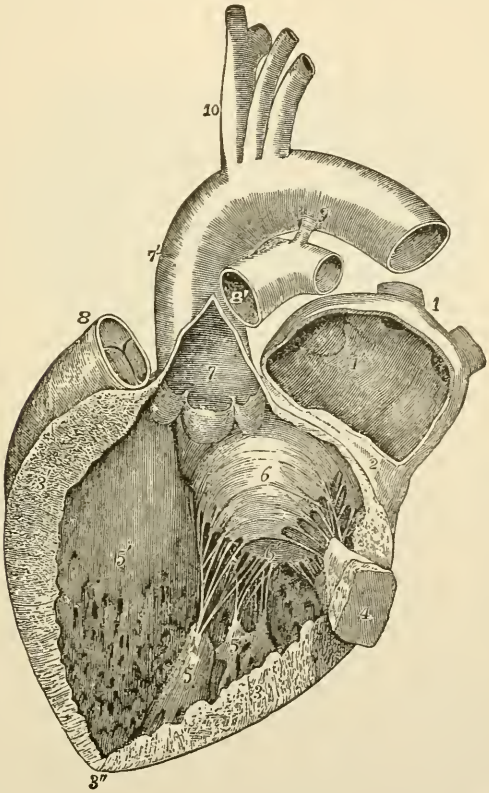
The right auricle and ventricle opened, and a part of their right and anterior walls removed so as to show their interior. ½. (QUAIN.)

side of the heart. The mitral valve, however (Fig. 90 and Fig. 91, 6, 6′), by which the left auriculo-ventricular orifice is closed, consists of two membranous folds instead of three, as is the case in the tricuspid valve, and is stronger than the latter.

It will be observed that the tricuspid and mitral valves open from the auricle toward the ventricle, but do not project from the ventricle into the auricle. At the anterior angle of the base of the right ventricle (Fig. 91, 7), may be seen an orifice guarded by three crescentic membanous folds, the semilunar valves. Through this orifice the right ventricle communicates with the pulmonary artery. The semilunar valves consist of doublings of the endocardium, strengthened by fibrous tissue. The convex border of each

valve is attached to the edge of the ring-like orifice of the pulmonary artery, the free edge projecting into the latter. Behind each semilunar valve the artery is dilated into a pouch, the sinus of Valsalva. This sinus prevents the valve when open from adhering to the walls of the artery, and enables the blood to get behind each valve and press it down so that the three valves meet (Fig. 91, 7), and so close the orifice, but readily separate when the flow is from

FIG. 90.



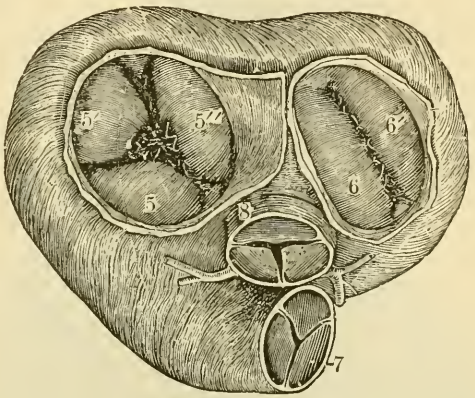
The left auricle and ventricle opened and a part of their anterior and left walls removed so as to show their interior. ½. The pulmonary artery has been divided at its commencement so as to show the aorta; the opening into the left ventricle has been carried a short distance into the aorta between two of the segments of the semilunar valves; the left part of the auricle with its appendix has been removed. The right auricle has been thrown out of view. (QUAIN.)

the ventricles toward the great vessels, preventing a reflux from the great vessels back into the ventricle.

At the middle of the free border of the semilunar valves may be seen a little nodule of fibrous tissue. These nodules, or corpora Arantii serve as a common central point of contact when the valves are closed. The semilunar valves of the aorta (Fig. 91, 8) do not differ in their structure or function from those of the pulmonary artery, and, like the latter, act when in contact in closing the orifice

of communication between the left ventricle and the aorta. The manner in which the tricuspid and mitral valves act can be readily demonstrated by filling the ventricles with water by means of a funnel introduced into the orifices of the pulmonary artery and aorta; the water rising up between the walls of the ventricles and the valves will float the valves up until their edges are approximated, so closing the auriculo-ventricular orifices. By pouring water into the pulmonary artery and aorta it will be seen that the water gets in between the wall of the vessel and the valve, into the

FIG. 91.



View of the base of the ventricular part of the heart, showing the relative position of the arterial and auriculo-ventricular orifices. ⅔. The muscular fibers of the ventricles are exposed by the removal of the pericardium, fat, blood vessels, etc.; the pulmonary artery and aorta have been removed by a section made immediately beyond the attachment of the semilunar valves, and the auricles have been removed immediately above the auriculo-ventricular orifices.

sinus of Valsalva, and so forces the free edges of the semilunar valves toward each other, thus effectually closing the orifices at the mouths of the great vessels.

Such being the general structure of the heart, let us consider now the course that the blood takes in passing through it. In watching the heart beating in a living animal, a mammal, for example, it will be observed that at the same moment the right auricle is dilated by the venous blood flowing from the system through the venæ cavæ, the left auricle is dilated by the arterial blood flowing into it through the pulmonary veins from the lungs. This synchronous dilatation of the auricles is known as the auricular diastole. Suddenly, and succeeding this auricular diastole, or filling up of the auricles, both auricles simultaneously contract, the venous blood passing from the right auricle into the right ventricle, the arterial blood from the left auricle into the left ventricle, regurgitation to any extent into the venæ cavæ or pulmonary veins being prevented by the muscular fibers encircling these vessels and the pressure of the blood. This synchronous contraction of the auricles is called the auricular systole. As in the experiment just performed with

the water, so the blood within the ventricles of the heart of the living animal gets in between the walls of the ventricles and the flaps of the tricuspid and mitral valves and floats the edges of the valves up until the auriculo-ventricular orifices are closed. At this moment, the ventricles being fully dilated simultaneously contract, with the effect of still more thoroughly approximating the tricuspid and mitral valves than is the case at the end of the auricular systole, and so of more completely closing the auriculo-ventricular orifices. The papillary muscles contracting at the same time as the walls of the ventricles and acting through the chordæ tendineæ upon the valves stiffen them and prevent their inversion into the auricles. The synchronous filling up and contraction of the ventricles is known as the diastole and systole of the heart, but more properly as the ventricular diastole and ventricular systole. During the ventricular systole the auricles are receiving blood from the venæ cavæ and the pulmonary veins.

Inasmuch as regurgitation backward from the ventricles into the auricles is prevented through the auriculo-ventricular orifices being closed by the approximation of the tricuspid and mitral valves during the ventricular systole, the venous blood passes from the right ventricle through the pulmonary artery to the lungs, and the arterial blood from the left ventricle through the aorta to the system. Immediately after the ventricular systole or contraction of the ventricles follows their relaxation. During this period the heart is in repose. The auriculo-ventricular orifices are again open, the venous and arterial blood that has accumulated in the right and left auricles respectively during the contraction of the ventricles and while the auriculo-ventricular orifices were closed, now flows into the ventricles, while this blood is replaced by the venous blood flowing into the right auricle from the venæ cavæ, and the arterial blood flowing from the pulmonary veins into the left auricle. Toward the end of the ventricular systole the venous and arterial blood, forced respectively into the pulmonary artery and the aorta, gets in between the walls of the vessels and the semilunar valves in the sinuses of Valsalva, and forces their free edges toward each other as in the experiment just performed with the water. At the end of the ventricular systole, the semilunar valves being closely approximated and the orifices of the great vessels closed, through the elastic recoil of the arteries on their contents, the blood, being unable to regurgitate backward from the pulmonary artery and aorta, is forced on to the lungs and the system. It will be seen from the phenomena just described that, while the right side of the heart containing venous blood is entirely distinct from the left containing arterial, nevertheless, the two sides of the heart act as one—the venous blood flowing into the right auricle as the arterial blood flows into the left, the synchronous filling up and emptying of the auricles being followed by the synchronous dilatation and contraction of the ventricles, at the same time the blood forced out of the

latter passing to the lungs and the system through the pulmonary artery and aorta respectively.

The beating of the heart, as we have endeavored to describe it, in an animal, a dog or a rabbit, for example, has been shown to be essentially the same in man, at least so far as comparison has been possible. As might be expected, cases of ectopia cordis are very rare, but there has been a sufficient number of such cases to demonstrate that the manner in which blood flows through the heart in man does not differ from that of the mammal.

While the action of the tricuspid valve and semilunar valves of the pulmonary artery is essentially the same as that of the mitral valve and semilunar valves of the aorta, nevertheless the valves on the right side of the heart do not close their respective orifices as perfectly as those on the left side of the heart, there being some little regurgitation possible back from the pulmonary artery to the right ventricle, and from the right ventricle to the right auricle. The effect of this insufficiency of the valves on the right side of the heart is obviously of advantage; were it otherwise, an excess of blood driven from the right ventricle through the pulmonary artery to the lungs might rupture those delicate organs. This danger is avoided through the imperfect closure of the pulmonary and the right auriculo-ventricular orifices, since, when resistance is offered by the pulmonary capillaries, the blood will regurgitate backward through the pulmonary artery to the ventricle and thence to the auricle. There is no insufficiency, however, on the left side of the heart, the auriculo-ventricular and aortic orifices being completely closed by the mitral and semilunar valves respectively. It will be observed also that the walls of the left ventricle are three or four times as thick as those of the right. This is due, as might have been anticipated, to the fact that the contraction of the left ventricle forces the blood to all parts of the system, whereas the right ventricle forces the blood only to the lungs. For the same reason the walls of the auricles are thinner than those of the ventricles, little force being required to drive the blood from the former cavities into the latter.

The muscular substance of the heart, like that of muscles generally, is therefore developed according to the amount of muscular force to be expended.

As the period which elapses in mammals during a cardiac revolution or cycle—that is, the time during which all the cavities of the heart fill and empty themselves—is only about one second, actually 0.8 sec. in man, it is evident that close and careful observation is necessary in order to distinguish the successive phenomena that we have endeavored to describe in the beating heart. It is well, therefore, to begin the study of the action of the heart by observing the phenomena, first, as they present themselves in the lower vertebrates, for example, in frogs, snakes, turtles, and alligators. Such animals are not only readily procurable, but are par-

ticularly suitable for the purpose, since in them the cardiac revolutions succeed each other much more slowly than is the case in mammals, and in the frog especially there is an appreciable interval between the systole of the auricle and that of the ventricle, whereas, in most mammals the systole of the auricle runs so into that of the ventricle that it is impossible to say exactly where the first ends and the second begins, the muscular contraction running as a continuous wave over auricle and ventricle from base to apex. Further, the heart of the frog has only one ventricle, and while there are two such cavities in the heart of the turtle, nevertheless, they communicate, the septum being but little developed. In these animals, then, the single ventricle acts like the two ventricles of the mammalian heart, and familiarizes one with the synchronous action of the ventricles when two such cavities are present. Again, these animals offer through their mode of breathing another advantage, in that the heart will continue beating even after the thorax has been opened, there being no necessity of keeping up artificial respiration. We shall see, however, when we wish to study the action of the heart in mammals, that artificial respiration must be maintained, for with the opening of the chest the lungs collapse, respiration ceases, and the circulation stops. Notwithstanding that, in mammals, a cardiac revolution occupies such a small period of time—about one second—nevertheless, the relative parts of the second elapsing during which the auricular and ventricular systole take place and the heart is in repose, have been experimentally determined, as in the horse, for example, by Marey and Chauveau.[1] The general results of their observations are embodied in

DURATION OF MOVEMENTS OF HEART IN HORSE.

Auricular systole.	Ventricular systole.	Repose.
0.2 sec.	0.4 sec.	0.4 sec.

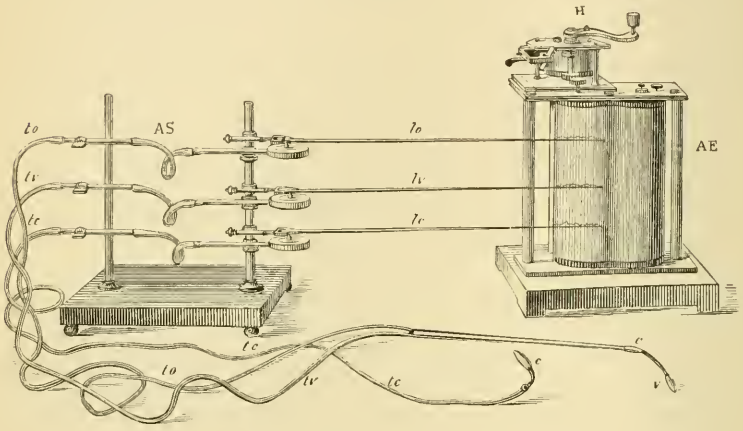
from which it will be observed that the auricular systole lasts two-tenths of a second, the ventricular systole four-tenths of a second, and the repose of the heart four-tenths of a second, one second being supposed to elapse during an entire cardiac revolution.

The apparatus necessary for the above determination of the rhythm of the heart's movements as they occur in the horse, as used by Marey, consists essentially of a sound (Fig. 92) to be introduced through the jugular vein into the heart of the animal. The sound is divided into two tubes, one of which is a distinct tube, the other being, however, only the space around the tube. The tube terminates at one end in a little elastic bag (*v*), to be inserted into the ventricle, and at the other end in a drum provided with a registering lever (*lv*). The space surrounding the tube communicates on the one hand with a similar elastic bag (*o*) to be inserted into the auricle, and at the other end with a tube passing into a

[1] Comptes rendus Soc. Biol., Paris, 1861. Comptes rendus Acad. Sciences, Paris, 1862.

drum provided with a second similar recording lever (*lo*). The object of the elastic bags *o* and *v* is that the successive contractions of the auricle and ventricle in which they are placed will be transmitted through them to the registering levers *lo* and *lv*, and as the auricle contracts before the ventricle it is evident that the lever *lo*

Fig. 92.

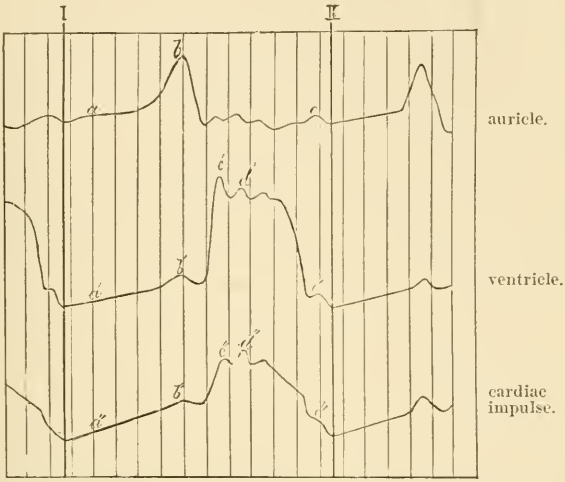


connected with the elastic bag (*o*) in the auricle will move before the lever (*lv*) connected with the bag (*v*) in the ventricle. If the registering levers are placed in contact with a recording surface (AE) moving at a uniform rate, and if this surface be marked by vertical parallel lines, each intervening space representing the one-tenth of a second, the lengths of time during which the auricular and ventricular systole and the repose of the heart last will be graphically recorded (Fig. 93). The cardiac revolution in this instance lasted twelve-tenths seconds.

In order to divide the surface of the recording cylinder into a number of spaces each equal to the one-tenth of a second, a vibrating reed (A) and an electro-magnet (B, Fig. 94) are used. The reed clamped under the electro-magnet by one end to a stand (C), the other end dipping into mercury (D), is connected on the one hand with a battery (E), and on the other with another small electro-magnet (F). Such being the disposition, at the moment that the current is made, the electro-magnet (B), being magnetized, will attract the reed, drawing it out of the mercury; but the current being thereby broken, the electro-magnet being then demagnetized, will cease to attract, and the reed will fall back into the mercury, remaking the current; the reed will then be again raised, the current broken, and the reed fall again into the mercury, the number of these alternate elevations and depressions per second depending upon the number of vibrations of the reed in that time. Inasmuch, however, as the small electro-magnet (F) is magnetized and

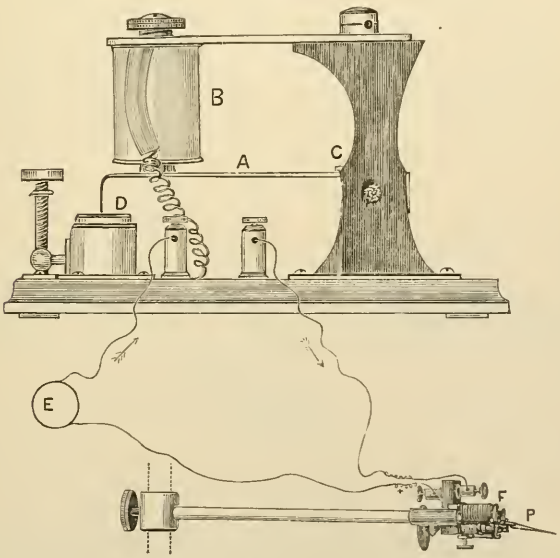
demagnetized in the same manner as the large one, the bar attached to it and carrying the pen (P) will approach and recede from it synchronously with the vibrations of the reed. By placing the pen in

FIG. 93.



Tracing the variations of pressure in the right auricle and ventricle, and of the cardiac impulse, in the horse. (To be read from left to right.) (MAREY.)

FIG. 94.



Vibrator.

contact with the recording cylinder, a trace is obtained in which the equal spaces between the vertical lines made by the marker are

equal to the one-tenth of a second, the reed used vibrating at that rate. By substituting reeds or tuning forks vibrating at the rate of 15, 20, 50, or 100 times a second, we get traces in which the equal spaces represent the corresponding fractional parts of a second. Usually, there is also a third registering lever (Fig. 90, *lc*) below the ventricular one, connected by tubing with a cardiograph (*c*), the object of which is to transmit the cardiac impulse caused by the beating up of the heart against the chest. This impulse is shown to be absolutely synchronous with the ventricular beat as recorded by the second lever (*lv*).

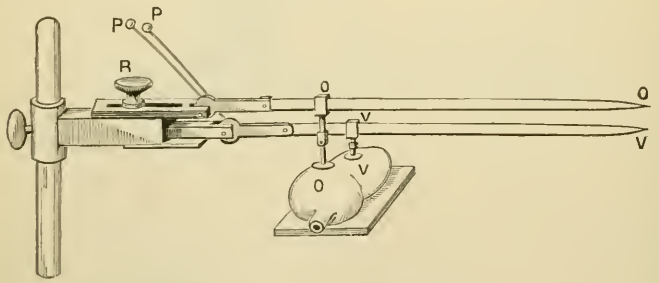
From the observations of Franck,[1] made upon a woman with ectopia cordis, there is no reason to doubt upon the supposition that the cardiac cycle lasts 0.8 seconds, that the duration of the auricular and ventricular systole and the repose of the heart are relatively the same in man as in the horse, as shown in

DURATION OF MOVEMENTS OF HEART IN MAN.

Auricular systole.	Ventricular systole.	Repose.
0.16 sec.	0.32 sec.	0.32 sec.

Inasmuch as it is by the contraction of the ventricles that the blood is driven through the lungs and the system and as the ventricles recover themselves, so to speak, during the repose of the heart it might be naturally supposed that when the number of the heartbeats are increased above the normal the duration of the repose of the heart would be shortened rather than that of the ventricular systole. That such is the case appears to have been shown experimentally both in man and animals. Thus it has been ascertained in man, by auscultation,[2] that the period elapsing between the first and the second sound of the heart, or the period corresponding, as

FIG. 95.



Double myograph.

we shall see, to the ventricular systole, varies much less in duration than that of the repose, with a varying heartbeat. Indeed, with a

[1] Travaux der Lab. de Marey, Tome iii., 1877, p. 311.

[2] F. C. Donders, Nederlandsch Archief Voor Genees en Natuurkunde, Tweede Jaargang, 1865, p. 139.

very rapidly beating heart the duration of the repose may be so brief that the contraction of the auricles practically follow that of the ventricles.

Experiments made by registering levers pressed upon the skin overlying an artery in man [1] or upon the exposed heart in animals [2] confirm the above conclusions. Thus, for example, with the heart beating in a man at the rate of 47 per minute the ventricular systole lasted 0.34 seconds, the repose 0.93 seconds, whereas with the heart beating at the rate of 128 per minute, the ventricular systole lasted 0.25 seconds, the repose only 0.21 seconds. A convenient method of demonstrating the time elapsing during the contractions of the auricles and the ventricles and the repose of the heart in a living animal, a frog or a turtle for example, is by means of the double myograph (Fig. 95). This instrument consists of two levers, to which are attached delicate rods, ending in aluminium plates, which rest upon the auricle and ventricle of the heart of the animal examined. The levers can be shortened or lengthened, their pressure diminished or increased by appropriate mechanical arrangements, and the movements of the auricle and ventricle transmitted by them are recorded upon a cylinder moving at a uniform and known rate, by which the time elapsing can be determined.

[1] E. Thurston, Journal of Anat. and Phys., Vol. x., 1876, p. 494.
[2] N. Baxter, Du Bois Reymond's Archiv, Band, 1878, s. 122.

CHAPTER XV.

CIRCULATION OF THE BLOOD.—(*Continued.*)

CARDIAC IMPULSE.

In examining the heart in a living animal, as described in the last chapter, it will be observed that with each ventricular systole the heart, as a whole, moves forward and upward, the apex more particularly beating up against the chest, and so giving rise to what is known as the cardiac impulse. If a finger be placed within the thoracic cavity of a living animal, between the heart and the side of the chest, with every contraction of the ventricle the finger will be pressed against the chest by the apex. Pathological cases, like that of the Viscount Montgomery, so graphically described by Harvey,[1] have given physiologists the opportunity of showing that the cardiac impulse is produced in men as in animals by the striking of the heart against the chest.

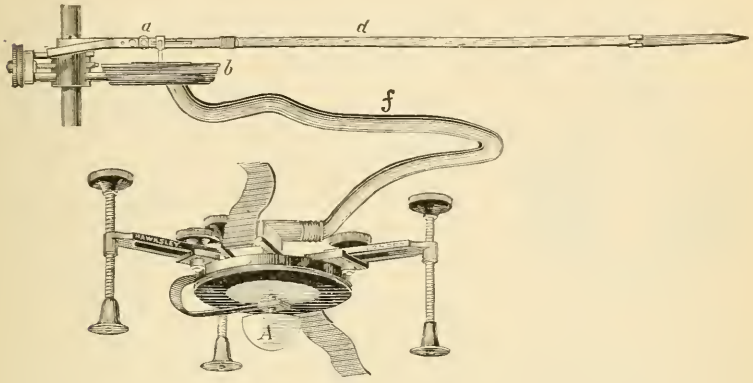
In man the cardiac impulse is most distinctly felt in the fifth left intercostal space, about two inches below the left nipple, and one inch to its sternal side. The force and extent to which the cardiac impulse may be perceived varies very much in different individuals, and in the same individual, according to circumstances. Thus, it is more perceptible in emaciated than in fat persons, during expiration than in inspiration, in one lying upon the left side than in one lying upon the right, etc. The movement of the heart forward and upward producing the cardiac impulse seems to be due to several causes. Thus, the sudden distention of the great elastic vessels at its base would throw the entire organ forward, the recoil of the ventricles, as they discharge their contents, further aiding the movement. The disposition of the muscular fibers is also such that the heart during its ventricular systole changes its form, bulging somewhat forward, the spiral muscular fibers, at the same time, tilting up the apex.

For ordinary purposes the force and extent of the cardiac impulse can be sufficiently well appreciated by the hand. The cardiograph, however, furnishes us with the means of a far more accurate study of the beat of the human heart than that afforded by the sense of touch alone. The cardiograph (Fig. 96) consists of a disk-shaped box, one side of which is formed by an elastic membrane. In the center of the latter is inserted an ivory knob (*A*), which is applied to the chest over the place where the cardiac impulse is greatest. The box, or tympanum, communicates by an elastic tube (*f*) with a second tympanum (*b*), with which is connected a registering lever

[1] Exercit. de generat. Animalium, p. 156. London, 1651.

(*d*). It is evident that when the cardiograph is firmly fastened to the chest that the shock of the cardiac impulse will be transmitted to the ivory knob, thence to the first tympanum and through the column of air in the communicating tube to the interior of the second tympanum, and so, by means of the elastic and movable lid

FIG. 96.



The cardiograph.

of the latter, to the registering lever. If the point of the lever be placed in contact with a cylinder revolving at a uniform rate, we obtain a graphic representation or trace of the heart's impulse (Fig. 97). By such an apparatus variations in the heart's beat, which

FIG. 97.

Tracing of heart's impulse in man, taken with cardiograph. To be read from left to right.

are so slight as to be quite inappreciable by the sense of touch alone, become very perceptible.

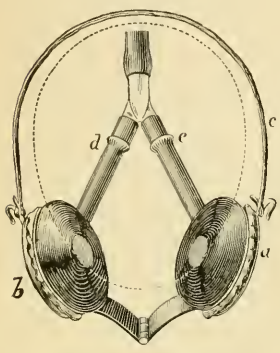
When it is desired to take a cardiographic tracing in a small animal, like a rabbit, guinea-pig, or cat, a very convenient form of cardiograph is that described by Marey[1] (Fig. 98). The instrument, as used by the author, consists of two tambours (*a*, *b*), each of which contains a spring, through which the membrane is kept projected. The two tambours are joined to one another pincer-like, by a hinge, and grasp the cardiac region on each side of the sternum. A girdle (*c*) attached by hooks to the tambours passes around the body of the animal, and secures the apparatus firmly. The compression of the air in the tambours due to the cardiac impulse is transmitted by the tubes (*d*, *e*) to a second tambour, to which is attached a recording lever, like that represented in Fig. 98. Fig. 99 gives the traces taken by this instrument.

It will be remembered that it was by means of the cardiograph

[1] Op. cit., p. 155.

and the sound introduced into the heart of the horse that Marey and Chauveau demonstrated experimentally that the cardiac impulse is absolutely synchronous with the ventricular systole. Whatever difference of opinion may exist as to the relative importance of the different causes assigned for the production of the cardiac impulse, there can be no doubt, then, that its immediate cause is the ventricular systole.

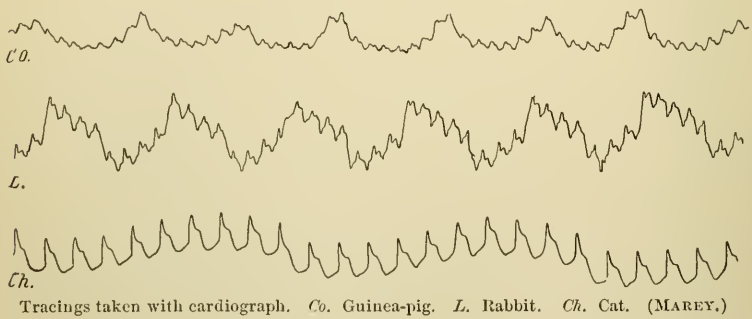
Fig. 98.



Cardiograph. (Marey.)

The spiral arrangement of the muscular fibers at the apex of the heart, already alluded to, explains another phenomenon accompanying the ventricular systole, the twisting of the heart. If the apex of the heart be closely watched, it will be noticed that the point twists upon itself from left to right with the systole, returning to its former position with the diastole. The heart, like a voluntary muscle, which it closely resembles in its substance, also hardens during contraction. This becomes very evident if the organ be grasped by the hand while beating. Like voluntary muscles, the heart also shortens during contraction. This can be demonstrated by quickly cutting the heart out of a living animal, pinning it down on a board by passing a needle vertically through its base, and then inserting a second needle into the board parallel with the first, so that the apex of the heart just touches the second needle. With each systole it will be seen that the ventricles invariably shorten, the apex distinctly receding from the second needle. If the beating heart be examined *in situ* there is, on the contrary, an apparent elongation of the heart during its systole. This is due, however, not to any

Fig. 99.



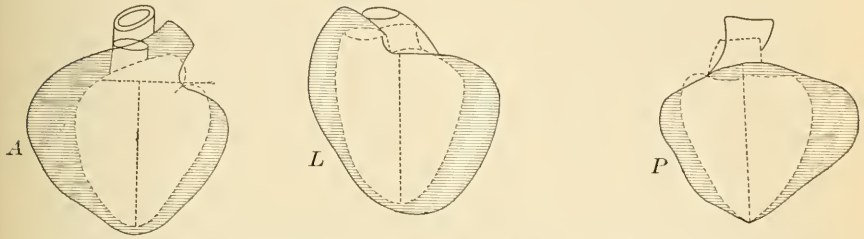
Tracings taken with cardiograph. *Co.* Guinea-pig. *L.* Rabbit. *Ch.* Cat. (Marey.)

elongation of the ventricles, but to the fact that at the moment of the cardiac impulse, which is synchronous with the ventricular systole, the whole heart, as we have seen, is moved forward and

protruded; at this moment the apex is apparently elongated, while, in reality, it is shortened.

However carefully the beating heart may be observed, it is, nevertheless, impossible, on account of the rapidity of its movements, to obtain a correct idea of the changes it undergoes in the living animal. Owing to this fact, plaster casts[1] (Fig. 100) have been

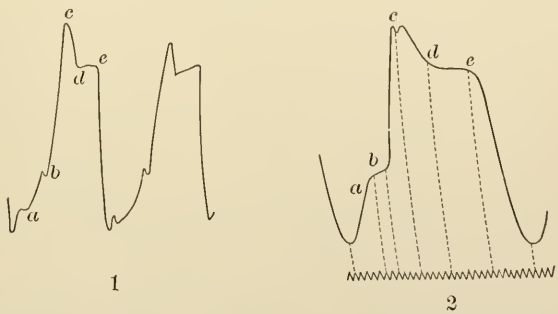
FIG. 100.



Projection of a dog's heart. Shaded portion indicates appearance of diastole; white portion, of systole. *A*. Anterior surface. *L*. Lateral surface. *P*. Posterior surface. (McKENDRICK.)

made of the distended and contracted heart fixed in that condition at the moment of death, which show, approximately at least, the changes undergone in the form of the heart in a living animal, and reveal the fact that the post-mortem form of the heart is not that of the living animal either in diastole or systole. It must be borne in mind that the changes in the form of the beating heart just described are such as occur in the opened chest, and necessitating also in the case of the mammal, the maintenance of artificial respiration. While there is no reason to suppose that the changes in the form

FIG. 101.



1. Cardiographic tracing from a case of ectopia cordis. (FRANÇOIS FRANCK.) 2. Cardiographic tracing from the exposed heart of a cat, obtained by placing a light lever on the ventricle. The tuning-fork curve marks 50 vibrations per second. (LANDOIS.)

of the heart observed in the unopened chest, Fig. 101, 1, differ essentially from those in the opened one, Fig. 101, 2, recent researches[2] render it possible that certain minor differences exist in

[1] F. Hesse, Du Bois Reymond's Archiv (Anatomie), 1880, s. 328.

[2] J. B. Haycraft, Journal of Physiology, V. xii., 1891, p. 448. J. B. Haycraft & D. R. Paterson, Ebenda, V. xix., 1896, p. 496.

the two cases. Thus, for example, it may be supposed that the ventricles contract more equably in all diameters, and that there is less flattening of the heart in the antero-posterior direction in the unopened chest than in the opened one.

Work done by the Heart.

In mechanics the work done by a machine is usually estimated in kilogramme meters or foot pounds, that is, the number of kilogrammes or pounds the machine can lift through one meter or foot. In other words, the work done equals the weight multiplied by the height. On the supposition that at each systole of the left ventricle, 180 grammes (6.3 oz.) of blood, the so-called "pulse volume," is ejected into the aorta under a pressure of 3.21 meters (10.2 feet), that being the height to which the blood would rise in a tube placed in the aorta of man,[1] the left ventricle lifts at each systole 180 grammes of blood, 3.21 meters high, that is, does 578.8 gramme meters of work ($180 \times 3.21 = 578.8$). If the 578.8 grammes be multiplied by 72 on the supposition that the heart beats seventy-two times a minute, and the quotient by 60 and 24 for the hour and day it will be seen that the work done by the left ventricle of the heart in twenty-four hours amounts to nearly 60,000 kilogrammeters $578.8 \times 72 \times 60 \times 24 = 5992704$0 gramme meters. Assuming that the work done by the right ventricle amounts to one-fourth of that done by the left, or 15000 kilogrammeters, the pressure of the blood in the pulmonary artery being one-fourth that of the pressure in the aorta, the work done by both ventricles during twenty-four hours would be nearly 75000 kilogrammeters (240 foot tons).[2] It should be mentioned, however, that the energy put forth by the ventricles of the heart is not only exerted in lifting 180 grammes of blood through 3.21 and 0.8 meters, respectively, at each systole, but in imparting to the blood the velocity with which it flows in the aorta and pulmonary artery. Assuming that the velocity in the aorta amounts to 0.5 meter per second, we can make use of the well-known formula $V = \sqrt{2gh}$ in which g is the accelerating force of gravity (9.81 meters per second) to obtain the value of h or the height through which the 180 grammes of blood must be lifted in order to acquire by falling from such height the given velocity. Squaring both sides of the equation $V = \sqrt{2gh}$ and transposing we obtain $h = \frac{V^2}{g} = \frac{0.25}{2 \times 9.81} = 0.0127$ meter. The work done by the left ventricle at each systole will be equal, therefore, to raising 180 grammes of blood 0.0127 meter high, for falling from that height the blood would acquire a velocity of 0.5

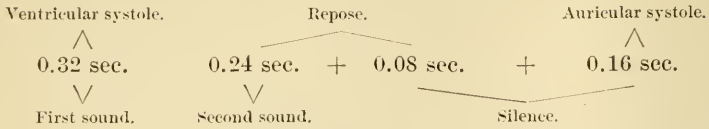
[1] Haughton, Animal Mechanics, 1873, p. 137.

[2] Kilogrammeters are converted into foot pounds by multiplying by 7.233. 1 kilo (2.2 pounds avoird.) raised 1 meter (3.2 feet) high = 1 lb. avoird. raised 7.233 high. Foot pounds are converted into foot tons by dividing by 2240.

meter. As the work done by the left ventricle in this respect is small, amounting in twenty-four hours to only 207.3 kilogrammeters, it is usually neglected together with that done by the right ventricle, which is necessarily still less, in estimating the work done by the heart. We shall see hereafter that, in accordance with the theory of the conservation of energy, that the work of 75000 kilogrammeters done by the heart in twenty-four hours is transmuted heat. Such being the case, 176263 heat units must be applied mechanically by the heart since 1 heat unit so applied will lift 425.5 grammes 1 meter high ($176263 \times 425.5 = 75000$ kilogrammeters). Further, as one gramme of coal when burned yields 8080 heat units, it follows that the heat transformed into work by the heart is equal to that which would be produced by the combustion within the heart of nearly 22 grammes of coal ($8080 \times 21.8 = 176263$). That the heat so transformed into work by the heart is not derived from the combustion of the carbon of its muscular tissue is shown by the fact that if so, the heart, upon the supposition that it weighs about 300 grammes, would be entirely consumed. It may be mentioned in this connection, though it will be considered hereafter, that as the energy exerted by the heart is expended in overcoming the resistance incidental to the circulation, the energy that disappears in being so applied reappears as heat.

If in a living animal the ear be applied to the precordial region, and in man more particularly to the third intercostal space a little to the left of the median line of the chest, accompanying the beat of the heart two successive sounds will be heard, followed by a silence. After a little practice it will be recognized that these two sounds differ from each other in their quality, pitch, and duration. The first sound is a dull, confused one, of a booming character, low in pitch, and lasts longer than either the second sound that follows it or the silence intervening between the second sound and the first one. The second sound as compared with the first one, is a clear sound, well defined, sharp, high in pitch. While, for all practical purposes, it may be said that the second sound immediately follows the first, there is quite an appreciable interval of silence between the second and the first sound, this interval of silence lasting about the same length of time as the second sound. On the supposition that 0.8 second elapses during the period in which the first and second sounds are heard and the silence, the first sound will last 0.32 second, the second sound 0.24 second, the silence 0.24 second. A comparison of the duration of the movements and sounds of the heart shows that the period of 0.32 second during which the first sound is heard is absolutely synchronous with the 0.32 second of the ventricular systole, that the 0.24 second during which the second sound is heard the heart is in repose, and that the silence is synchronous partly with the last 0.08 second during which the heart is in repose and partly with the 0.16 second of the auricular systole.

DURATION OF MOVEMENTS AND SOUNDS OF HEART DURING 0.8 SECOND.



From the fact of the first sound of the heart being composed of both a valvular and muffled character it might be naturally supposed that it consists of more than one component and that its production must be due therefore to more than one cause. Such, indeed, has been shown to be the case, the first sound being made up in reality of two sounds, a valvular one caused by the closure of the auriculo-ventricular valves and a muffled one due to the contraction of the muscular fibers of the ventricles. That the first sound is so produced is shown by the fact that it is heard during the period of the ventricular systole during the time that the auriculo-ventricular valves close and the muscular fibers contract. That the closure of the auriculo-ventricular valves contributes to the production of the first sound can be further demonstrated by experiments like those of Chauveau and Faivre,[1] who either modified the first sound or abolished it altogether by preventing the closure of these valves by cutting the chordæ tendineæ, or introducing a wire ring into the auriculo-ventricular orifices, and by the recent ones of Wintrich[2] who demonstrated by means of a resonator and stethoscope that the first sound consisted of two components of different pitch.

Further, pathology shows that, in man, the character of the first sound is changed if the auriculo-ventricular valves are diseased, and it is well known, also, that in auscultation the first sound is heard with its maximum intensity over these valves, and that it is propagated downward along the ventricles to which they are attached toward the apex.

That the muscular contraction of the heart produces a sound, can be demonstrated by the cardiophone (Fig. 102), a distinct sound being heard when the latter is attached to the telephone, and that the sound so produced contributes to the production of the first sound of the heart can be proved by experiments such as those of Ludwig and Dogiel,[3] Krehl,[4] Kasem-Bek,[5] in which the valves were made incompetent and the only way of accounting for the sound still heard was to attribute it to muscular contraction.

While some difference of opinion still prevails as to the nature

[1] Nouvelle recherches experimentales sur les Mouvements du Cœur, etc., p. 30. Paris, 1856.

[2] Sitz-berichte der phys. med. soc. zu Erlangen, 1873, s. 1, 1875, s. 51.

[3] Berichte u. die Verhandl. d. K. Sächsinn, Gessel. der. Wissen. zu Leipzig, 1868, s. 89.

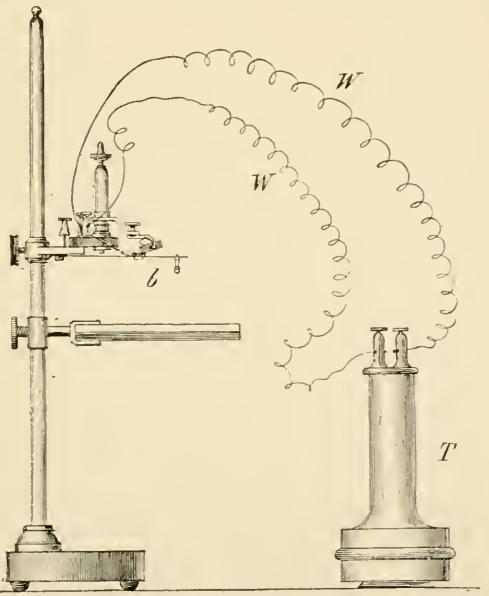
[4] Archiv für Anat. u. Phys., 1889, s. 253.

[5] Pflüger's Archiv, Band xlvii., 1890, s. 53.

of the sound produced by cardiac or skeletal muscle, it appears to be due to a repetition of the unequal tensions that occur in a muscle during its contraction, rather than of individual contractions, which we shall see hereafter, constitute the condition of tetanus.

As has already been observed, the second sound differs from the first in being a clear, well-defined sound, and is essentially of a

FIG. 102.



Cardiophone. *b*. Button to be placed upon heart. *W*, *W*. Wires for attachment to telephone. *T*. Telephone.

valvular character. It is heard during the first three-quarters of the period in which the heart is in repose. Now, at this moment the semilunar valves of the pulmonary artery and aorta are flapping together through the blood getting in between the valves and the walls of the vessels. The closure of these valves will account for the second sound of the heart and its simple valvular character. The second sound of the heart can be imitated by suddenly closing the aortic valves by a column of water, as was first shown by Rouanet,[1] and can be abolished by hooking back the semilunar valves in a living animal, as was first demonstrated by Williams, and confirmed by the Dublin Committee in their report presented to the meeting of the British Association in 1836.[2]

We learn also through the changes produced in the character of the second sound of the heart from disease of the semilunar valves,

[1] J. Rouanet, Analyse Des Bruits Du cœur, These No. 252, Paris, 1832, p. 9.

[2] Report of the Sixth Meeting of the British Association for the Advancement of Science, London, 1837, pp. 261, 275.

and from auscultation that the second sound is heard most distinctly opposite the semilunar valves, and is propagated upward along the great vessels to which they are attached. There can be no doubt, then, that the second sound of the heart is caused simply by the closure of the semilunar valves of the pulmonary artery and aorta.

It may be mentioned in this connection that when the heart beats more rapidly than usual, the period of silence is shortened rather than the periods during which the two sounds are heard, just as we saw the period of repose of the heart is shortened rather than that of the systole.

When it is considered that age, sex, food, exercise, etc., influence the rapidity of the action of the heart, it becomes evident that an intimate sympathy must exist between the circulation and the other great functions of the economy. From time immemorial, therefore, the frequency of the heart's action has always been regarded as one of the most important indications of the general health of the system. The practical importance, therefore, of determining, as far as possible, the average beat of the heart in a given time, within the limits of health, must be obvious to every physician. We shall see in the next chapter that with each ventricular systole or cardiac impulse there is an expansion of the arteries due to the blood being forced out of the left ventricle into the aorta. This expansion of the arteries or pulse, which we will consider again in detail, is, for convenience' sake, usually felt and counted instead of the beat of the heart itself, and, other things being equal, the result of such examination can be accepted as a criterion of the condition of the heart and vascular system generally. It will be observed from the Table compiled from the observations of Guy [1] and Milne Edwards,[2] that the average number of cardiac beats per minute varies according to the age and sex, and this should always be remembered when the pulse is counted in man. Thus in the fœtus, while the number of pulsations per minute is 140 (determined by listening to the fœtal heart), at birth the number falls to 136, and that up to the third year of life, while the pulse is still the same in both sexes, it now averages only about 107 beats to the minute. As we pass, however, from infancy to youth, it will be seen that the number of pulsations per minute gradually diminishes, and that at the same period the pulse of the female is a little quicker than that of the male. In adult life the average number of pulsations in the male may be said to be from 70 to 72 per minute, and from 6 to 8 beats more in the female. At the approach of old age the pulse becomes a little more frequent, at eighty years of age the number of beats usually being about 80 a minute.

As is well known, in animals of different species, but which are closely allied in their general organization, the pulse varies with the size of the animal, being slowest in the largest and fastest in the

[1] Cyclopædia of Anat. and Phys., Vol. iv., p. 181.
[2] Physiologie, Tome iv., p. 62.

FREQUENCY OF HEART'S ACTION.

Age.	Pulsations per minute.	
	Male.	Female.
Fœtal	140	140
At birth	186	136
1 year	128	128
2 years	107	107
2 to 7 years	97	98
8 " 14 "	84	94
14 " 21 "	76	82
21 " 28 "	73	80
28 " 35 "	70	78
35 " 42 "	68	78
42 " 49 "	70	77
49 " 56 "	67	76
56 " 63 "	68	77
63 " 70 "	70	78
70 " 77 "	67	81
77 " 84 "	71	82

smallest animals. Thus in the horse the number of beats is only 40 to the minute, in the ass about 50, in the sheep from 60 to 80, the dog 100 to 120, in the rabbit 150, and in some of the smallest rodents even 175. The circulation is also more rapid in small insects than in large ones, and it has long been a matter of observation that in man the pulse is slower in persons of large stature than in those of small. This connection between the rapidity of the pulse and the size of the animal seems to be a very general one in the animal kingdom, so far as has been observed, and its significance will become apparent when we study the production of animal heat in the economy, for we shall see then that the rapidity of the circulation is directly correlated with the production of energy, and that, as a general rule, the greatest amount of nervo-muscular activity is exhibited by the smallest animals of any one order rather than by the largest ones.

This dependence of the pulse on the size may to a certain extent explain the difference between the pulse of the young and of the old, and of the sexes as just mentioned. It should be stated, however, that the observations of Volkmann[1] show that youth and sex in themselves, without regard to size, influence the rate of the pulse, for in individuals of equal size the youngest had the quickest pulse, and the pulse of the woman was always quicker than that of the man.

It must not be forgotten, however, in counting the pulse that often individuals are met with in perfect health in whom the pulse is extremely rapid, or just the reverse. Thus, according to the late Professor Dunglison,[2] the pulse of Sir William Congreve never fell below 128 beats per minute, while, as is well known, on the other hand, that of Napoleon I. often did not exceed 40 beats to the min-

[1] Die Hæmodynamik, s. 30, 36. Leipzig, 1850.
[2] Human Physiology, 1856, 8th ed., Vol. i., p. 446.

ute.[1] Haller[2] refers to cases where the pulse was still slower, being only 23 beats to the minute.

As is well known, the action of the heart is also influenced by digestion; according to Milne Edwards,[3] there is an increase of from five to ten beats after each meal. On the other hand, prolonged fasting diminishes the frequency of the pulse from twelve to sixteen beats. According to the same high authority, while vegetable food diminishes the action of the heart animal food increases it, fermented drinks at first diminish then accelerate the movements of the heart. Coffee is, however, in the highest degree a cardiac stimulant. Every one is familiar with the fact that any violent exercise, like running or jumping, increases the action of the heart. As long ago as the early part of the last century it was shown, by the experiments of Bryan Robinson,[4] that the pulse of a man in the recumbent position being 64 to the minute, was increased to 78 during a slow walk, and still further increased to 100 by walking a league and a-half in an hour, and rose as high as 140 to 150 after running as rapidly as possible. It is also well known, from the experiments of Guy,[5] that if the number of pulsations on the average be 66 to the minute in a man lying down, the number will be increased to 71 if he sits up, and will be still further increased to 81 if he stands up. After what has just been said in reference to muscular activity increasing the action of the heart, the results of Guy's experiments are just what might have been expected, since muscular force is developed in changing the position of the body and maintaining it in equilibrium.

Indeed, it was in this way that many of the older physiologists theoretically explained the acceleration of the heart's beat observed in the change of posture just referred to. It was Guy, however, who first demonstrated, by means of a revolving board which supported the person who was the subject of the experiment and so relieved him of the necessity of supporting himself by muscular exertion, that the variations in the frequency of the heart, according to the position of the body, was dependent upon the quantity of muscular force put forth in maintaining equilibrium in each of the positions. The practical importance of these facts for the physician cannot be exaggerated, since it is obvious that, in a person suffering with heart disease, it is of the utmost importance that any increase in the action of the heart should be avoided. The greatest caution, under such circumstances, should be advised in the taking of exercise; any sudden or violent effort, like quickly lifting up a trunk, or running rapidly up stairs, should be strictly prohibited, the slight acceleration in the heart's beat from such an effort being frequently a cause of death in persons affected with heart disease.

It is well known that during the day there is a variation in the

[1] Berard, Physiologie, Tome iv., p. 113.
[2] Elementa Physiologie, Tome ii., p. 256.
[3] Physiologie, Tome iv., p. 79.
[4] A Treatise on the Animal Economy, p. 177. Dublin, 1732.
[5] Cyclopædia of Anat. and Phys., Vol. iv., p. 188.

action of the heart, and for a long time it was supposed that the pulse was quicker in the evening than in the morning. According to the older physiologists, "Pulsus nocturnus multo celerior est."[1] When, however, the action of the heart at evening is considered uninfluenced by food, exercise, etc., it has been found that the pulse at that period of the day is really slower than in the morning, and that the heart is less susceptible to the action of stimulants. This condition is due, no doubt, to muscular fatigue.

In sick persons, however, it is otherwise, since at evening there is usually some fever present, and this is accompanied by a quicker pulse. According to Milne Edwards,[2] while sleep tends to diminish the action of the heart, the number of pulsations at least in man, is not diminished to any extent by that circumstance. In women, and especially children, in that condition, however, there seems to be considerable difference as compared with the wakeful state. The temperature of the surrounding atmosphere influences also the rapidity of the action of the heart—heat increasing and cold diminishing the number of heart beats.

De la Roche[3] found that his pulse was increased to 160 beats per minute in an atmosphere of 65.5° C. (150° F.), and it is well known that the pulse is quicker in hot countries than in cold ones. Among the other influences that accelerate or diminish the action of the heart must be mentioned that of respiration. When the manner in which the blood flows through the pulmonic capillaries, and the changes produced in it, have been described, the mutual sympathy existing between the heart and lungs will then be fully appreciated. It would be anticipating too much to give a detailed account of this mutual influence at present, but it may be mentioned in this connection that the action of the heart may be voluntarily arrested through modifying the conditions of respiration. Thus, for example, if after a forcible expiration the mouth and nose are closed and then a powerful inspiratory effort is made, the heart may cease to beat. This appears to be due to the extreme dilatation of the heart caused by the venous blood flowing so freely into the right side of the heart as to cause engorgement of the lungs and of the left side. On the other hand if exactly the opposite experiment is tried, that is, if after taking a deep inspiration, and the mouth and nose are closed, a strong expiratory effort is then made, the heart's action may also be arrested.

Under these circumstances the heart is contracted, since the flow of the venous blood is interrupted, as shown by the veins of the neck and face swelling up, while the arterial blood is forced out of the compressed lungs into the left ventricle and thence into the arteries. Both of these experiments are dangerous, and should not often be repeated. It is well known that the late Prof. E. F. Weber, of Leipsic, was able, by closing the glottis and at the same time con-

[1] Keill, Teutamina medico-physica, p. 178. London, 1730.
[2] Physiologie, Tome iv., p. 74. [3] These, Paris, 1806, p. 33.

tracting forcibly the chest, to diminish the cardiac beats to three to five a minute, which were unaccompanied with the cardiac impulse or sounds, and with the result, finally, of stopping the action of the heart altogether. On one occasion, having suspended his respiration longer than usual, Professor Weber[1] fell into a syncope. This case, concerning the truth of which there can be no question, confirms the statements made by Galen,[2] and others,[3] that death in certain individuals had been caused by the voluntary suspension of their breathing. One of the most interesting and best authenticated cases of the possibility of temporarily arresting the action of the heart was that of Colonel Towhnsend, reported in the early part of the last century by Cheyne.[4] This physician relates how Colonel Towhnsend could so arrest the breathing and the beating of his heart that death was simulated. In this condition the pulse could not be felt at the wrist; there was no cardiac impulse; a mirror placed in front of the mouth was not tarnished, and, apparently, he was dead. On the occasion reported by Cheyne, Colonel Towhnsend remained in this condition for half an hour; gradually, however, the respiration and circulation became reëstablished. It should be mentioned, however, that Colonel Townhsend died later in the afternoon of the same day that the facts just described occurred.

It may be mentioned in this connection as appropriately as elsewhere that if a wide glass tube filled with smoke be inserted into one nostril, the other nostril and mouth being closed, that the smoke will move with each beat of the heart. The "cardio-pneumatic movement," as this movement is called and of which a tracing can be obtained by appropriate apparatus, appears to be due to the fact that the heart occupying less space within the thorax when it contracts air will pass into the lungs with each systole and out with each diastole.

Having described the motion of the heart and the various influences that modify it it remains now to consider, so far as is known, how the beat of the heart is maintained. When we come to the special study of muscular contractility we shall learn that an ordinary voluntary muscle usually contracts in response to a stimulus, the will, emanating in the brain, and transmitted through a nerve to the muscle.

While the heart is a muscular organ, its action differs from that of the ordinary muscle in being involuntary in character. The voluntary muscle, however, not only contracts through the influence of the will or nerve force, but also in response to mechanical, electrical or chemical stimuli, and, in this respect, the heart does the same. Thus, if the chest of a living animal be opened, and the heart mechanically irritated by an instrument, a scalpel, for example, it will be seen to contract like any other muscle stimulated in

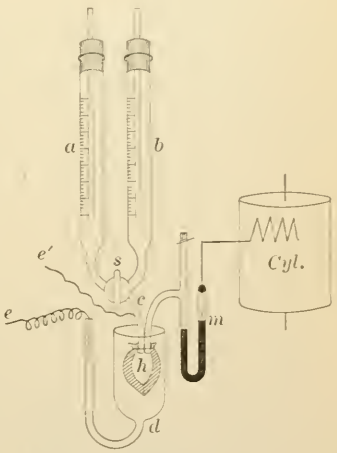
[1] Milne Edwards, Physiologie, Tome iv., p. 88.
[2] Œuvres trad. de Daremberg, Tome i., p. 366.
[3] Müller's Archiv, 1851, s. 91.
[4] The English Malady, p. 307. London, 1734.

a similar manner. The same effect follows the application of electricity by means of the electrodes. The addition of warm water, and exposure to the air will also cause the heart to contract.

The muscular substance of the heart, then, like that of any other muscular organ, is endowed with the property of contractility, through which the organ contracts in response to various stimuli. There appears to be no doubt that the contractions of the heart are maintained by a constant supply of oxygenated blood, anæmia of the heart, brought about by the ligature of the coronary arteries, promptly arresting the heart's action,[1] whereas, as shown long ago by Haller[2] and numerous observers[3] in recent times, the heart will continue to beat for many hours if supplied with blood. As the blood, however, is a highly complex fluid, it becomes a matter of importance to determine, if possible, the constituent or constituents upon which the maintenance of the muscular contractions of the heart more particularly depend. Unfortunately, however, the difficulties that have obtained until recently in isolating the mammalian heart have been so great that little has been learned as to the influence exerted by any one constituent of the blood upon the heart.

The influence exerted by the different constituents of the blood upon the contraction of the frog's heart can, however, be shown by means of a frog-manometer, such, for example, as that of Kronecker. This apparatus consists (Fig. 103) of a two-way canula (*c*) which is tied into the excised heart. The canula (*c*) communicates, by one limb with a mercurial manometer (*m*), and by the other with the Marriotte flasks (*a*, *b*). Either *a* or *b* can be put in communication with the interior of the heart. The fluid in one of the flasks contains the substance whose effect upon the heart is to be studied, the fluid in the other, being an indifferent one, is used as a control fluid. The glass vessel (*d*) contains fluid in which the heart pulsates. One of the electrodes (*e'*) is attached to the canula, the other electrode (*e*) is inserted into the fluid in *d*. Of the different substances studied, such as oxygen, sodium carbonate, sodium and potassium chloride, salts of calcium, oxygen appears to be highly important, if, indeed, not essential, more oxygen being

Fig. 103.



Scheme of Kronecker's frog-manometer. *a*, *b*. Marriotte's flasks for the nutrient fluids. *s*. Stop-cock. *c*. Canula. *m*. Manometer. *h*. Heart. *d*. Glass cup for *h*. *e'*, *e*. Electrodes. *Cyl*. Revolving cylinder. (Landois.)

[1] Erichsen, London Medical Gazette, 1842, 2d Ser., Vol. ii., p. 561.

[2] Memoires sur la Nature Sensible et Irritable des Parties du corps animal a Laussanne, 1756, Tome i., p. 370.

[3] N. Martin, Phil. Trans., 1883, Part ii.

used by a beating than a resting heart, and the amount of oxygen consumed being greatest during work. Sodium carbonate is of great value in maintaining the alkalinity of the blood. Sodium chloride appears to be essential and should exist in isotonic amount. Salts of calcium appear to be essential, since precipitation of the calcium by a soluble oxalate brings spontaneous contraction of the heart to a standstill. In conclusion, it may be mentioned that a mixture consisting of tri-calcium phosphate, sodium chloride, potassium chloride, and sodium bicarbonate, in proper proportions,[1] will maintain the contractions of the heart for many hours.

It is a matter of daily observation that the circulation, like the other functions, is influenced by the nervous system, but as the relation of the nervous system and the circulatory organs is quite a complex one, the consideration of this part of the subject will be for the present deferred.

In concluding our account of the heart it may be now appropriately mentioned, however, that while the action of the heart is greatly influenced by the nervous system, the heart itself is insensible. The insensibility of the heart is often observed in cases where it has been wounded, the patient being unconscious of pain, or, indeed, of any feeling at all. In the celebrated case of the Viscount Montgomery, so often mentioned by authors, and so well described by Harvey, the opportunity was offered of directly inspecting and feeling the heart. Harvey tells us, in the work[2] already referred to, that this individual was entirely unconscious of the application of his finger to the heart.

[1] S. Ringer, Journal of Physiology, Vol. vii., 1886, p. 291.
[2] Op. cit., p. 375.

CHAPTER XVI.

CIRCULATION OF THE BLOOD.—(*Continued.*)

THE ARTERIES.

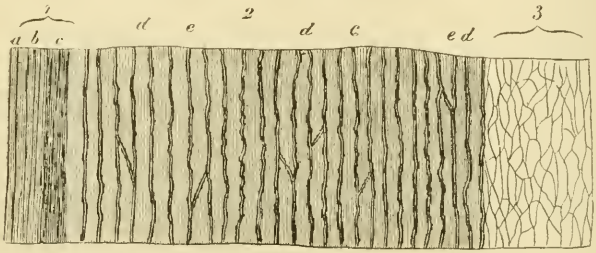
We have seen that at each ventricular systole the blood is forced from the heart into the pulmonary artery and aorta. The manner in which the venous blood passes through the pulmonary capillaries, and returns aërated arterial blood to the heart, will be described when the subject of respiration is considered; for the present let us follow the blood as it flows through the aorta and its branches, the arteries.

The arterial system, by means of which the blood is circulated to all parts of the body, consists of musculo-elastic tubes, which, in their general disposition, may be compared to a cone of which the heart is the apex, and the base the periphery of the body, or to a tree of which the aorta represents the trunk, and the arteries the branches. As we recede from the heart to the periphery the branches divide and subdivide, and anastomose, until, becoming microscopic, they pass into the capillaries. With few exceptions, the combined calibre of the branches of an artery is greater than that of the artery itself. There is a gradual increase, therefore, in the capacity of the arterial system as we pass from the heart to the capillaries. As a general rule, the arteries run in nearly a straight course to the parts which they supply with blood. The branches gradually diminish in size, and comparatively few are given off between the main trunk and the capillaries. The aorta and the arteries, like the heart, are not nourished by the blood circulating in their cavities, but by blood from adjacent vessels, the vasa vasorum, which have no direct connection with the arteries which they supply. The vasa vasorum, which include little veins, as well as arteries, are mostly restricted to the outer coat of the artery, but few penetrating the middle coat. The vasa vasorum of the arteries bear the same relation to the arteries that the coronary arteries and veins bear to the heart itself. The arteries are also supplied by nerves derived from both the cerebro-spinal and sympathetic systems, but principally from the latter. The manner in which these nerves modify the calibre of the arteries will be understood when their minute structure has been studied, to the consideration of which let us now turn.

The arteries, including the aorta, consist essentially of three coats (Fig. 104), an external fibrous, a middle elastic muscular, an internal epithelial. Each of these coats, however, can be shown to consist of several subcoats, or layers, more or less developed, according to the size and situation of the artery.

The external or fibrous coat of the artery is mainly composed of fine bundles of white connective tissue, the filaments of which are usually disposed in a spiral manner around the vessel, and on the surface are often loosely adherent to surrounding parts; the inner surface of the fibrous coat, however, is intimately blended with the middle coat. Between the bundles of the connective tissue fibers, of which the external coat consists, are disposed in various amounts fine nets of elastic tissue; these nets are most abundant in the inner part of the external coat. To their internal coat the arteries owe chiefly their strength. The middle coat of the artery consists of layers of elastic and muscular tissue, which are disposed around the vessel in a circular manner. The relative amount of these tissues, however, varies according to the size and position of the vessel. In the largest arteries, those nearest the heart, the middle coat is com-

FIG. 104.



Transverse section of the walls of the aorta, treated with acetic acid, and magnified. 1. Internal coat. *a*. Epithelium and basement membrane. *b*, *c*. Layers of elastic tissue. 2. Middle coat. *d*. Layers of elastic tissue. *e*. Muscular and connective tissue. 3. External coat, composed of fibrous tissue and fine nets of elastic tissue. (LEIDY.)

posed mainly of elastic tissue, there being very little muscular tissue present, whereas, in the medium size arteries, the middle coat chiefly consists of muscular tissue, and in the smallest arteries of muscular tissue only. The muscular tissue is of the unstriated character, and consists of fusiform cells, or bands, with oval nuclei; they do not entirely surround the artery; the elastic tissue forms a more or less close network of fibers, which, from its membranous perforated character, is often known as the fenestrated membrane. A great deal of the elasticity, and all the contractility with which the arteries are endowed, are due to their middle coat.

The internal coat of the artery is essentially a continuation of the endocardium, or lining membrane of the heart, and consists of three layers, an outer elastic of the membranous fenestrated kind, a middle basement membrane, and an inner endothelial layer, composed of elongated lozenge-shaped cells. The outer elastic layer of the internal coat of the artery is intimately connected with the inner portion of the middle coat, while the inner endothelial membrane is that part of the artery which ultimately becomes the capillary. We have seen that the action of the heart is intermittent

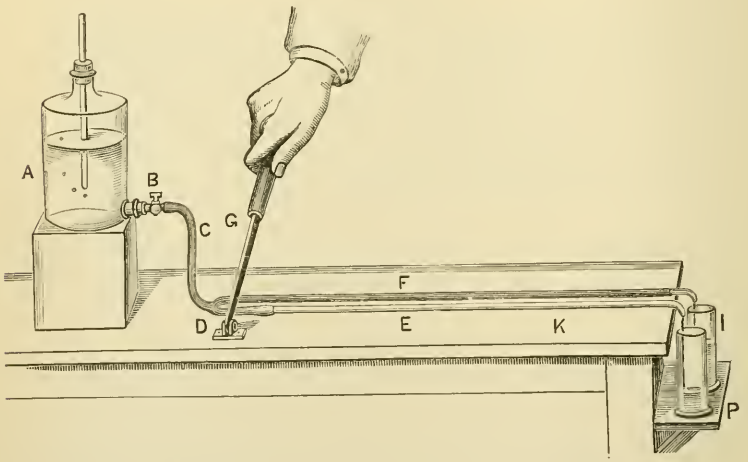
in character, each ventricular systole being followed by the diastole, a period of repose during which no blood flows into the arterial system from the heart. If, however, a large artery near the heart be opened, it will be observed that the blood flows out of the artery continuously, both during the systole and diastole. With each ventricular systole, however, the jet becomes stronger; the flow in the artery, therefore, is not, like that in the heart, intermittent, but remittent. If the artery examined be situated, however, at a distance from the heart, near the periphery, the flow of the blood will be found to be but slightly remittent, indeed almost uniform, while finally, as we shall see in the capillaries, it is entirely so. The flow of the blood, then, as it passes from the heart through the arteries to the capillaries from being intermittent becomes remittent, and finally uniform. It is to the property of elasticity, with which we have seen arteries are endowed, that this transformation of an intermittent motion into a remittent one is due. For, during each ventricular systole, of the blood that is forced into the arteries a part only presses onward the blood already in the arteries, the remaining part presses outward the walls of the artery. From the moment, however, that the effect of the systole ceases—that is, during the diastole—through its elasticity the walls of the artery recoil on the blood which has distended them, and press it onward (the aortic valves preventing any regurgitation) immediately after the part of the blood that has just preceded—that is, the part forced forward during the systole. There are two successive waves of blood then in the artery, that of the systole and that of the diastole; they follow each other, however, so rapidly, that ultimately they merge into one, the movement of the blood in the capillaries becoming finally uniform. The elasticity of the artery favors, therefore, the onward movement of the blood.

Did the arteries consist of rigid tubes the blood would flow through them in the same intermittent manner as it does through the heart. With each ventricular systole blood would flow from the arteries into the capillaries in an amount equal to that which flowed from the heart into the aorta, with the diastole of the heart, however, the flow from the arteries would entirely cease. The author is in the habit of demonstrating the difference between the flow of liquids in elastic and rigid tubes by means of the apparatus represented in Fig. 105. This consists of a reservoir (A) containing a colored fluid, and provided with a stopcock (B) by means of which the delivery of the fluid can be regulated. To the stopcock is connected a flexible, but, if possible, a non-elastic tube (C) which is connected with a tin tube (D), the latter bifurcating so that the fluid from the reservoir can pass through the tube G into the tubes E and F, simultaneously. One of these tubes (E) consists of glass, the other (F) of caoutchouc, the former (E) is connected with the tube D by caoutchouc. At their distal ends the tubes D and F are bent downward so that the fluid flowing from them can

be conveniently collected in the jars P I. The glass tube, as it terminates, is drawn out so as to simulate the capillary end of an artery, its orifice having a diameter of 2.5 mm. ($\frac{1}{10}$ of an inch). The same effect is accomplished, as regards the caoutchouc tube, by inserting into its distal end a tube of glass of the same length and diameter as that of the distal end of the glass tube. The tubes E F are supported by, and firmly bound to, the table K, which is painted white, so that the colored fluid can be readily seen in the glass tube.

The reservoir being filled and the stopcock turned on, the colored fluid passes into the bifurcated tube and thence through the elevation and depression of the lever (G), worked by hand, in an intermittent manner, into the rigid glass tube and elastic caoutchouc one. The lever should be uniformly depressed and elevated at the rate of about sixty times to the minute and the fluid watched as it escapes from the tubes. It will be observed, from the reasons

FIG. 105.



Apparatus to demonstrate the flow of a fluid through rigid and elastic tubes. (MAREY.)

already given, that the flow from the rigid glass tube is absolutely intermittent, with each depression of the lever the flow entirely ceasing. On the other hand, the flow from the caoutchouc tube is distinctly remittent, the jet not ceasing but only diminishing with the depression of the lever and increasing again with its elevation. It is needless to add that the elevation and depression of the lever represent the opening and closing of the aortic valves, the escape of the fluid from the tubes the flow of blood through the constricted arteries toward the capillaries.

This experiment not only proves that the elasticity of a tube influences the character of the movement of the fluid flowing through it, but also of the quantity that escapes from it, for if the jars P I be

examined, it will be seen that the one collecting the liquid from the elastic tube is almost three times as full as that collecting from the rigid one. During an experiment lasting three minutes, while 2800 c. cm. (3.7 pints) of fluid flowed into the one jar, only 1000 c. cm. (1.7 pints) flowed into the other. This is as might have been expected when it is remembered that an elastic tube is capable of receiving more fluid than a rigid one, for two reasons: first, there is not only the quantity of fluid which, after entering the tube, presses directly onward and which corresponds to the fluid in the rigid tube, but also an additional quantity which presses the walls of the elastic tube outwardly. It is this lateral fluid, so to speak, that follows and adds itself to the part which presses directly onward that converts the intermittent motion into the remittent one, and by just so much as the walls of the tube will give to this lateral pressure the amount of fluid entering the elastic tube will be in excess of that entering the rigid one. Second, it being remembered that the principal obstacle to the flow of a liquid through a tube is the friction of its walls, and that the friction is proportional to the square of the velocity of the current, it follows that as the effect of the dilatation of the artery is to diminish the velocity of the current through it, and therefore to diminish the amount of friction according to the square of the velocity of the current, the quantity of fluid delivered from the elastic tube will, therefore, be greater than that from the rigid one.

We have seen that the arteries are not only endowed with elasticity, but also with contractility or tonicity, as it was called by Bichat, and it has been shown, experimentally, by Poisseuille,[1] that the recoil of the walls of the artery upon the blood that had previously distended it is greater than can be accounted for by the elasticity of the artery alone. Indeed, the tendency of an artery is always to contract, to empty itself of its blood. For this reason difficulty is always experienced in injecting the vessels of an animal immediately after death.

If, during life, the calibre of the arteries is about equal to that observed after death, it is because the arteries are during life distended with blood.

That the arteries will contract independently of the elasticity or the recoil following upon the distention of its walls through the blood forced into the vessel by the heart can be demonstrated by ligating an artery in two places and in a part of its course where no branches are given off, so as to exclude the influence of the general circulation, and then opening the artery at a point situated between the ligatures. Under such conditions, although the artery is uninfluenced by the action of the heart, etc., the blood will jet out with force, and the artery will be almost completely emptied. When it is remembered, as we have seen, that in the smallest arteries the middle coat consists entirely of muscular fibers, there being

[1] Journal de Magendie, T. ix., p. 44.

no elastic tissue present, it becomes evident that the contractility, in such cases at least, must be due entirely to the action of the muscular fibers. Hence the distinction clearly made by John Hunter,[1] that in the large arteries the recoil of the walls was due almost entirely to the elasticity; in the smallest arteries, on the contrary, to the contractility. The physiological significance of this distinction was also seen, Hunter attributing to the elasticity the conversion of the intermittent action of the heart into the remittent one of the artery, to the contractility the regulating of the calibre of the arteries, and, therefore, the supply of the blood to the system. Inasmuch as arteries therefore contract in virtue of their contractility as well as of their elasticity, and as after death the contractility disappears, as might be expected, the amount of contraction is greater in the living artery than the dead one. The contractility of the arteries can be easily demonstrated by the application of various stimuli, mechanical, chemical, electrical, exposure to air, application of cold, etc. Thus the mere scraping of the walls of an artery or the pricking of a needle will cause them to contract. Various chemical substances, such as sulphuric acid, ammonia, alum, and ergot, are among the most powerful stimuli to muscular contractility. Indeed, the usefulness of hæmostatics in arresting hemorrhage depends upon this property.

The smallest arteries readily contract under the influence of both the direct and indirect electrical currents. Simple exposure of the arteries to air suffices to produce a slow but permanent constriction of the vessel. The local application of cold—ice, for example—in stopping bleeding after wounds, is well known to the uneducated, the effect being due to contractility. The stimulus of great heat produces the same result.

We have already seen that, through nervous influence, the arteries contract. In speaking of the structure of the arteries, it was mentioned that the muscular fibers are supplied by nerves derived from the sympathetic and cerebro-spinal systems. The stimulation by electricity of these vasomotor nerves, as they are called, is followed by contraction of the arteries they supply, while division or paralysis of these nerves is followed by a dilatation of the vessels. The phenomena of blushing, of sudden pallor in the face, are familiar examples of the influence of the vasomotor nerves in modifying the amount of blood in a part; in the one case the vessels dilating, in the other contracting. When it is remembered that more blood is demanded by an organ at one time than another, a gland when secreting, for example, requiring more arterial blood than when quiescent, it becomes evident that there must be some means in the economy, by which the amount of blood supplying any organ can be varied. It is through the vasomotor filaments that the nervous system modifies the calibre of the arteries, and, in that way, regulates the amount of blood distributed to different

[1] Works, Vol. iii., p. 194.

parts of the body. The origin and distribution of the vasomotor nerves will be considered in detail hereafter.

While it must be admitted that the contractility of the arteries favors somewhat the onward flow of the blood within them, without doubt the principal effect of their contractility is the regulation of the supply of blood through the modification of their calibre. It should be mentioned, as regards this contractility, that, by whatever means it is induced, whether the stimuli be mechanical, chemical, or electrical, that, unlike ordinary striated muscle, it does not immediately follow the application of the stimulus, more or less time intervening, according to the stimulus used. It is also to be noticed that a temporary relaxation usually follows a contraction, and, if the stimulus be very intense, the contraction is followed by a dilatation, as if, for the moment, the contractility had been exhausted in producing its effect.

We have seen that during each ventricular systole the aorta and arteries generally become distended with the blood forced into them by the heart, and as the pressure of the blood is exerted both laterally and longitudinally, the artery must therefore enlarge in both these directions. The longitudinal enlargement of the artery is, however, so much more apparent than the transverse one, as will be explained presently, that the latter is usually masked or obscured. So much so, indeed, is this the case, that for a long time it was denied by physiologists that there was any transverse dilatation of the artery. While Harvey,[1] it is true, states that when an artery is divided, and held at the cut-end by the fingers, the dilatation is apparent, it must be admitted, however, that, to the ordinary eye, this is far from evident. The proof of the transverse dilatation of the artery, however, does not rest on the mere assertion of a physiologist, however celebrated, but can be readily demonstrated, either as shown by Flourens,[2] by placing around a living artery a watch-spring, the ends of which just meet during the relaxation of the vessel, and which separate during the lateral distention, or, by Poisseuille's[3] method, which consists in enclosing an artery in a living animal within a tube filled with water (the ends, of course, being closed), and the interior of which communicates with a capillary tube, serving as an indicator, in which the water rises or falls, according as the water is forced out of the tube by the lateral distention or transverse dilatation of the artery, or is sucked back again by the recoil of the wall of the vessel, due to its elasticity. The longitudinal expansion of the artery, or the elongation, is more easily demonstrated than the expansion in the transverse direction. As also shown by Flourens it is very evident, if the artery examined be slightly colored, and a needle as a guide be immovably placed on one side of the vessels with each ventricular systole and diastole the colored point on the artery will be observed to advance and recede in a longitudinal direction. The elongation of the ar-

[1] Exercitatio altera ad J. Riolanum Opera Omnia, 1756, p. 112.
[2] Annales des Sciences Nat., 1837, T. vii., p. 106. [3] Op. cit., T. ix., p. 46.

tery is also very apparent in the vessels of the stump of an amputated extremity, and becomes quite evident in a vessel in which the blood flowing meets with an obstacle, as where the artery bifurcates, or runs in a tortuous course rather than a straight one. During the elongation of an artery the vessel frequently rises up out of its bed, experiencing considerable displacement; this is known as the locomotion of the artery, and is often seen in the temporal and radial arteries of old and emaciated persons.

On account of the extent of the vessel exposed during the elongation, the longitudinal expansion is far more evident than the transverse one, and, as we have already observed, quite obscures it. The increase of capacity due to the longitudinal expansion of the artery is, however, less than that due to the transverse one, for, as is well known, the capacity of the tube increases as regards the length, in a simple ratio only, whereas, the capacity of the tubes in the transverse direction increases not in a simple ratio, as the diameters, but as the squares of the diameters.

The elongation and transverse dilatation of the arteries due to the distention of their walls by the blood forced into them by the heart at each ventricular systole constitute the pulse. It will be observed that the pulse, or the expansion of the artery, is synchronous with the contraction of the ventricle of the heart, not with the heart's expansion, as was thought by Galen, and the ancients generally. Although this truth seems to have been known to a writer who lived during the early part of our era, it remained for Harvey to demonstrate it in modern times. Ordinarily, neither the elongation nor transverse dilatation of an artery or its pulse is visible to the naked eye, or appreciable even by touch alone. It is for this reason that the observer presses with his finger more or less the artery examined, thereby constricting the vessel and so increasing the velocity of the blood, it flowing faster as the artery becomes smaller, the same amount of blood passing through in a given time; this, as we have seen, increases friction, and so causes an obstacle to the flow, which, within limits, increases the force of the heart, and, therefore, the distention of the artery, and so makes the beating of the vessel or the pulse more apparent.

Production of the Pulse.

No artery in man can be directly measured, either as regards its expansion or its pressure. In feeling the pulse, however, the endeavor is made to measure both by the sense of touch alone.

While the experience of every physician shows to what an extent slight variations in the pulse can be appreciated by the tactus eruditus alone, nevertheless it is only by means of the graphic method that the conditions on which the production of the pulse and its variations depend can be successfully investigated. By the graphic method, as we have seen, a pictorial representation, a trace of some kind of the phenomena occurring, can be obtained and pre-

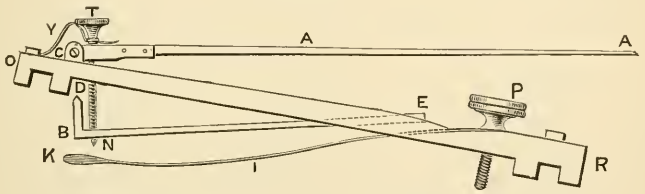
served, by means of which slight variations, due to change of conditions, become at once evident that would be entirely unappreciable by the eye or touch unaided.

The advantage of such an experimental investigation of the pulse, the practical application that can be made of it in investigating the cause of disease, will be at once appreciated after the sphygmograph and the arterial schema, the apparatus we use in studying the pulse, has been described, and the results obtained by it shown.

The Sphygmograph.

The object of the sphygmograph (*σφυγμος*, a trace, and *γραφω*, to write) is to measure the succession of the alternate dilatations and contractions of an artery due to the blood forced into it by the beating heart, to magnify these movements, and to register them on a surface moving at a uniform rate by clock-work.

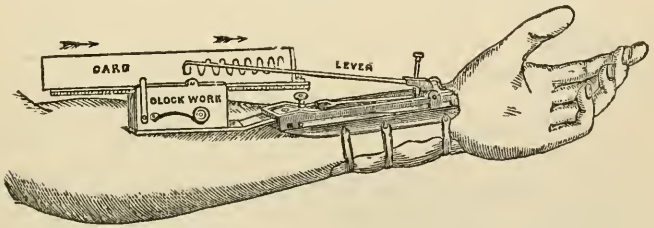
FIG. 106.



Mechanical arrangement of the sphygmograph. (SANDERSON.)

The sphygmograph was originally invented by Vierordt, and afterward greatly improved by Marey. The instrument (Fig. 106) consists of a brass frame (O R), the under surface of which is covered with ebonite, and which can be applied to the outer edge of the volar aspect of the forearm so that it rests immovably in this position with reference to the radius and wrist-bones, particu-

FIG. 107.

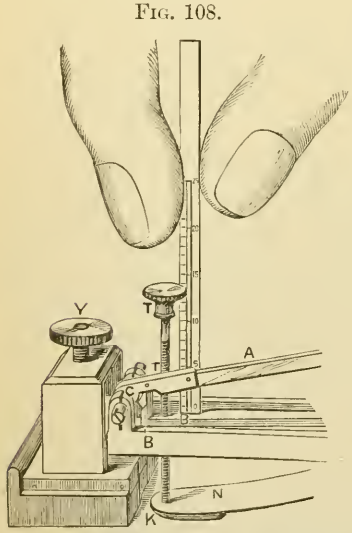


Marey's sphygmograph applied to arm. (MAREY.)

larly the scaphoid. The pulsations of the radial artery are received by an ivory button (K), placed at the free end and under the surface of the steel spring I; the other fixed end of the spring is attached to the brass work at P. By means of the ivory button and

spring the pulsations of the artery are transmitted to the vertical screw T, which passes through the brass bar N, whose center of motion is at E, above the attachment of the steel spring I; the free end (B) of the brass bar is bent upward at right angles, and carries a knife-edge (D), Fig. 106. The elevation of the screw T, through the pulsations of the artery, raises the brass bar N, carrying the knife-edge D, the latter, in turn, elevating the registering lever A, of which one end (C) is supported by a horizontal rod passing through it and connecting the sides of the brass frame, while the other movable end (A) terminates in a metal joint, which registers the motion of the pulsation on a piece of paper (Fig. 107) blackened by passing it to and fro through the flame of a kerosene lamp. The paper is fastened to a copper plate, which is moved at a uniform rate by the clock-work (Fig. 107). As the distance between the supporting rod C and the knife-edge D is much less than the length of the lever, the vibrations of the extremity of the lever (A) are far more extensive than the vertical movement of the spring I and screw T. By means of the screw T the distance between the steel spring I and the registering lever A can be varied at will without interfering with the mechanism by which the movement is transmitted. The distance between the brass frame and the ebonite surface can also be increased or diminished, according to the direction in which the screw Y is turned, and, in this way, the pressure on the artery may be varied; the variation in the pressure is measured by the scale (Fig. 108), which has been experimentally graduated by turning the instrument upside down, and successively placing a series of weights on what would be ordinarily the lower surface of the spring, but which is now the upper surface, and observing the extent of its deflection and marking the scale correspondingly. Finally, by means of a movable clamp, there can be adapted to the sphygmograph, when desirable, a delicate tympanum, with registering lever, in connection with a cardiograph, so that the traces of the cardiac and arterial pulsation can be registered simultaneously on the blackened surface.

Fig. 108.

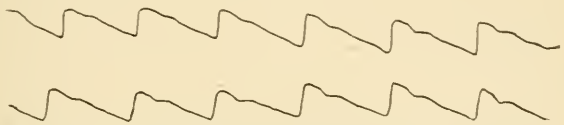


Scale for determining pressure excited by artery. (SANDERSON.)

To take a trace with the sphygmograph of the radial artery, which is the vessel usually examined, the forearm should be supported on something, a table, for example, the back of the wrist resting on a

cushion or padding, so that the dorsal surface of the hand will be inclined, with reference to the forearm, at an angle of 20 to 30 degrees. The instrument must be so placed on the wrist that the block rests upon the trapezium and scaphoid, while the extremity of the spring is opposite the styloid process of the radius, the general direction of the sphygmograph will then be parallel with that of the radius. In making an observation it is best to begin by adjusting the instrument so that the ivory button on the under surface

FIG. 109.

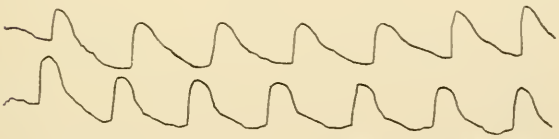


Sphygmographic tracing from radial artery of a man æt. twenty-five.

FIG. 110.

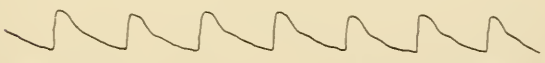
Sphygmographic tracing from radial artery of a man æt. thirty.

FIG. 111.



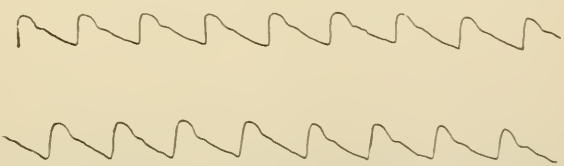
Sphygmographic tracing from femoral artery of a man æt. thirty.

FIG. 112.



Sphygmographic tracing from radial artery of a woman æt. sixty-five. Atheromatous arteries.

FIG. 113.



Sphygmographic tracing from radial artery of a man æt. seventy. Atheromatous arteries.

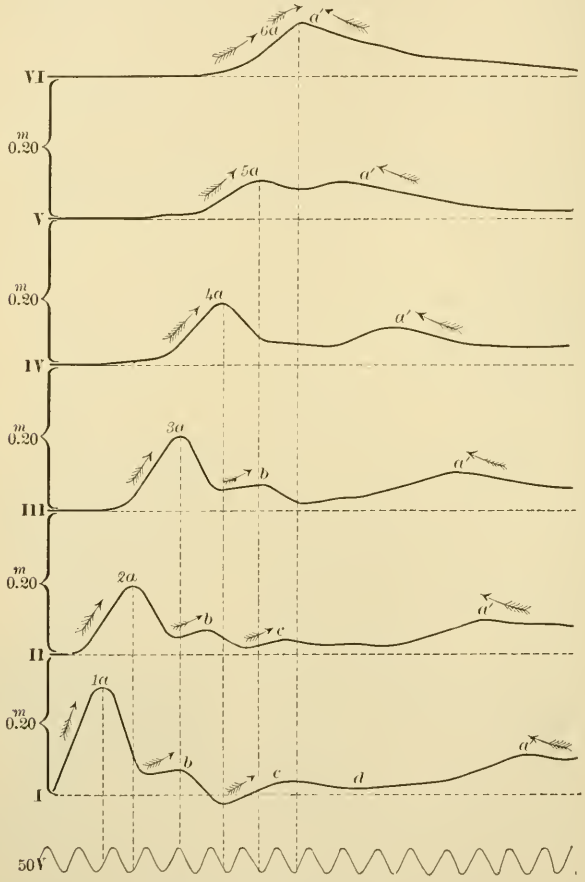
of the spring is at such a distance from the bone that the artery is pressed upon during its entire expansion, and yet not so compressed as to obliterate at any moment its cavity.

To those unfamiliar with the use of the sphygmograph, perhaps it will be well to begin by arranging the spring so that it will exert a pressure sufficient to flatten the artery against the radius and then

to diminish the pressure until the effects of such compression disappear, and thus to take traces of the maximum and minimum pressures, and one then of an intermediate character.

Having described the sphygmograph and the manner of using it, the following figures will illustrate the character of the traces taken

Fig. 114.



Pulse-curves described by a series of Sphygmographic Levers—placed at intervals of 20 cm. from each other along an elastic tube into which fluid is forced by the sudden stroke of a pump. The pulse-wave is travelling from left to right, as indicated by the arrows over the primary (*a*) and secondary (*b*, *c*) pulse-waves. The dotted vertical lines drawn from the summit of the several primary waves to the tuning-fork curve below, each complete vibration of which occupies 1-50 second, allow the time to be measured which is taken up by the wave in passing along 20 cm. of the tubing. The waves *a'* are waves *reflected* from the closed distal end of the tubing; this is indicated by the direction of the arrows. It will be observed that in the more distant lever VI. the reflected wave, having but a slight distance to travel, becomes fused with the primary wave. (From Marey.)

by it. Thus, for example, Figs. 109, 110, and 111 are obtained from the radial and femoral arteries in a healthy man of about thirty years of age. Figs. 112 and 113 are from the radial of a

woman æt. sixty-five and of a man æt. seventy respectively, in both of which cases the arteries were in an atheromatous condition.

If sphymographic tracings from arteries such as shown in Figs. 109–113 be compared with those obtained from an india-rubber tube, Fig. 114, through which water is forced by a pump and upon which sphygmographs are applied at equal intervals, the tracings will be seen to present in both cases the same general characters. In both, the same kind of movements succeed each other in the same order. With the expansion of the artery and the tube the levers rise, with the contraction they fall, then the secondary elevation or dicrotic pulse occurs, then finally the descent again. As in the case of the natural heart, so in that of the pump it will be observed that, as long as the heart and pump act, the respective valves being open, the artery and tube expand, and the levers ascend, and with the cessation of the flow of liquid from behind the artery and tube contract and the levers descend.

Inasmuch as the curves obtained from the artery and the india-rubber tube by sphygmographic methods are essentially of the same character it may be reasonably inferred that they are produced in the same way. It is for this reason that tracings, such as are represented in Fig. 114, may be used as illustrating the conditions upon which the production of the natural pulse depends. It is obvious that what we call the pulse is due not to a movement of the blood itself which is one of translation and slow but to the expansion of the wall of the artery following the systole of the heart, and which beginning at the aortic orifice progresses wave like towards the capillaries. "Unda non est materia progrediens sed forma materiæ progrediens."[1] It need hardly be mentioned that a sphygmographic tracing is not a representation of a pulse wave since the ascending part of the curve only indicates that the pulse wave is passing under the sphygmograph, the descending part that the wave has passed by. It will be observed that the ascending part of sphygmographic tracing or curve is steep, the descending part gradual. The steep ascent is due to the sudden expansion of the wall of the artery following the ejection of blood by the heart, the gradual fall to the recoil of the arterial wall due to its elasticity not being instantaneous. The lever remains, therefore, momentarily at the height to which it has been elevated by the pulse wave, this period being prolonged in proportion as the elasticity of the artery is diminished. Hence, in old persons in whom the arteries are not very elastic the curve at the summit is rounded off and the descent is a gradual one. It will also be observed from an inspection of successive sphygmographic traces, such as are represented in Fig. 114, that the ascending part of the curve becomes less steep in proportion as the position of the sphygmographs recede from that of the pump or heart. This is also in accordance with the explanation of the manner in which the pulse wave is produced just given.

[1] E. H. Weber, De pulsu in omnibus arteriis plane non synchronico, Annot Acad. Leipzig, 1834.

It was shown by Weber that the pulse wave is transmitted at a rate of about 9 meters (28.8 feet) a second. Weber[1] determined this velocity by observing with chronometers the difference in time of the beat of the facial and dorsalis pedis arteries, measuring the distance of the facial artery from the heart as accurately as possible, and the distance of the dorsalis pedis from the facial, and subtracting the first distance from the second, the difference of distance the pulse wave passed over in the second case, as compared with the first, will account for the difference in the time of the beats, and give approximately the distance passed over by the pulse wave in one second. Supposing that the ventricular systole lasted four-tenths of a second, the length of the pulse wave would be $\frac{4}{10}$ of 9 meters = 3.6 meters (11.5 feet), and there would be, therefore, two and a-half waves in a second $\left(\frac{9}{3.6} = 2.5\right)$. Consequently the anterior end of a pulse wave would have reached the extremities before the posterior end had left the left ventricle. It would appear, however, that this estimate of the length of the pulse wave is somewhat exaggerated, it having been shown by the photosphygmograph that the pulse wave is about 1.5 meters (4.7 feet) long, requiring, therefore, about one-sixth of a second to pass from the heart to the foot. As a certain length of time elapses during the transmission of the pulse wave from the heart to the capillaries, it is obvious that the pulse will be felt in arteries near the heart sooner than in those far from it. This is well shown in the successive sphygmographic traces of Fig. 114, a considerable interval of time elapsing between the elevation of lever 1, placed near the pump and lever 6, at some distance from it. Any one can readily convince himself, in his own person, that there is a gradual retardation of the pulse from the heart to the periphery, by feeling the left carotid artery with the thumb and index finger of the left hand, and the left radial with those of the right. The beat of the radial artery will be felt later than that of the carotid, the difference in the time of the beat being quite appreciable.

When it is remembered that, as the blood is propelled forward into the arterial system, it is being continually diverted laterally through the distensibility of the walls of the arteries, and that as the quantity of blood forced forward at each ventricular systole is limited in quantity, it must follow, as we recede from the heart to the periphery, that there will be less and less blood forced forward. The blood having been progressively absorbed, so to speak, by these lateral distentions in the proximal portion of the arteries, there will be less, therefore, to distend the distal parts. The pulse being due to this distention, must, therefore, be weaker in the arteries at a distance from the heart than in those near it, and must ultimately disappear in the smallest arterioles altogether. As a fact, the pulse is rarely felt in arteries having a diameter less than $\frac{1}{3}$ of a mm. ($\frac{1}{7}\frac{1}{5}$ of

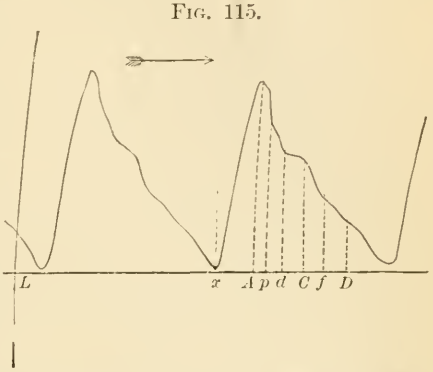
[1] Muller's Archiv, 1851, s. 537.

an inch). It is for this reason that in the case of an aneurism, the lateral distention being here greatly exaggerated, that the pulse is often absent in that portion of the artery situated beyond the seat of the disease. In the case of aneurism of the aorta, the pulse may be absent in all of the arteries of the body.

From the very nature, therefore, of the production of the pulse it must not only be postponed, but sooner or later extinguished. It will be seen from an examination of the pulse tracing of the radial artery of man that the lever, after having descended some distance from its maximum elevation, rises again and then descends finally.

The secondary crest *C* (Fig. 115) superimposed upon the primary curve constitutes, as already mentioned, the dicrotic crest, and the pulse giving rise to it the dicrotic pulse. When two extra crests appear, which is sometimes the case, the pulse is said to be tricrotic, and when several are seen, polycrotic. Usually, when extra crests appear, one or more, they are situated upon the descended part of the curve, and the latter is then spoken of as being katacrotic. In some cases, however, as in aneurism of the aorta (Fig. 116), for example, the primary crest does not appear at the highest part of the curve, but upon its ascending part, the curve being then called anacrotic.

Fig. 115.

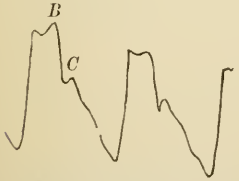


Pulse Tracing from the Radial Artery of Man.

The vertical curved line, *L*, gives the tracing which the recording lever made when the blackened paper was motionless. The curved interrupted lines show the distance from one another in time of the chief phases of the pulse-wave, viz., *x* = commencement and *A* end of expansion of artery. *p*, pre-dicrotic notch. *d*, dicrotic notch. *C*, dicrotic crest. *D*, Post-dicrotic crest. *f*, the post-dicrotic notch. These are explained in the text later on. (Foster.)

It may be mentioned in this connection that in well marked cases of dicrotic pulse the dicrotic crest is not only well defined, but also the pre-dicrotic and dicrotic notches preceding it, and the post-dicrotic crest and notch following it as shown in Fig. 115. Difference of opinion still prevails among physiologists as to the exact manner in which the dicrotic pulse is produced. According to some investigators it is due to the pulse wave being reflected back from the capillaries or small arteries to the heart. If this were the case, however, the distance between the dicrotic and primary crests ought to be less in arteries far from the heart than in those near to it, since the distance passed over by the retrograde wave will be less in the former

Fig. 116.



Anacrotic sphygmograph tracing from the ascending aorta. (Aneurism.) (Foster.)

than in the latter. As it has been shown, however, by measurement that the distance between the dicrotic and primary crests is the same in both the peripheral and proximate arteries, which is inconsistent with the theory of the dicrotic pulse being due to a retrograde wave, it is obvious that the latter must be produced in some other way. At the present day the dicrotic pulse is usually supposed to be due to a secondary wave which, being generated at the aortic valves, is thence propagated towards the periphery, the wave being produced in the following manner: At the end of the ventricular systole, the pressure in the ventricle being less than in the aorta, the blood flows back towards the heart and closes the semilunar valves, the latter through their resistance thereby give rise to the secondary wave, which, following in the wake of the pulse wave, gives rise to the dicrotic pulse. In connection with the production of the dicrotic pulse it may be mentioned that the conditions favoring it are an elastic extensible arterial wall, a low mean pressure permitting readily the action of the arterial wall and a quick contraction of the ventricle with the ejection of a comparatively large quantity of blood.

While the description of the pulse in disease belongs rather to works on medicine and therapeutics, it may not appear superfluous to mention that pathology confirms the views that have just been offered as to the production of the natural pulse. Thus, in an ossified artery, there is no pulse, because dilatation is impossible. When the arteries near the heart are rigid, the pulse is jerky, and the flow of blood is intermittent, not remittent. We see the same kind of pulse when the walls of the arteries are relaxed, unable to recoil thoroughly on their contents. If the artery be irritable, and at the same time distensible, the pulse will be exaggerated, and can be seen by the naked eye when, otherwise, it is usually imperceptible. The character of the pulse is profoundly affected by the conditions of the system, modified by general disease. Thus the large compressible pulse of fever, the hard pulse of Bright's disease, the small pulse of peritonitis, the soft pulse of collapse, etc., are well known to the physician.

Finally, it has been shown by Vierordt and Aberle[1] that there is a daily variation in the calibre of the arteries that must influence somewhat the character of the pulse, the radial artery, for example, being larger in the evening than in the morning.

[1] Archiv. f. physiol. Heilkunde, 1856, B. xv., s. 574.

CHAPTER XVII.

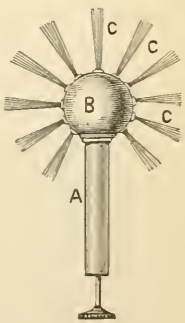
CIRCULATION OF THE BLOOD.—(*Continued.*)

PRESSURE AND VELOCITY OF THE BLOOD IN THE ARTERIES.

By blood pressure, whether it be cardiac or arterial, etc., is meant the pressure or force that is exerted by the blood upon the surface of the vessel containing it, or, what is the same thing, the force that is required to be put forth by the walls of the vessels in order to sustain the column of blood within them. Before showing the manner in which the blood pressure is determined in a living animal, let us first endeavor, however, to illustrate, by a few simple experiments, the manner in which the pressure of liquids in general is determined.

It is well known, as first shown by the distinguished geometrician Pascal, that the pressure exerted anywhere upon a mass of liquid, assuming the latter to be perfectly fluid and uninfluenced by gravity, is transmitted undiminished in all directions, acting with the same force on all equal surfaces, and in a direction at right angles to those surfaces. That the force exerted upon the mass of a liquid is transmitted in all directions, and at right angles can be readily shown by means of the apparatus represented in Fig. 117. This consists of a cylinder provided with a piston fitting into a hollow sphere pierced with numerous holes, into which are fitted small cylindrical jets placed perpendicularly to the sides. The sphere and cylinder being filled with water, and the piston depressed, the water will be observed to spout out from all of the jets, and not simply from the one opposite the piston. In order to show that the pressure is transmitted, not only in all directions, but equally, we make use of an apparatus very similar to the one just described, and represented in Fig. 118, it differing only in that the perpendicular jets projecting from the sphere contain closely fitting, but easily movable pistons, each piston having the same area. The sphere being filled with water, the latter, by virtue of its weight, will press equally upon the surface of all the pistons. Neglecting the influence exerted by the weight of the water, and the friction of the pistons, it will be observed that if a given pressure (P) be exerted upon the piston A the water will transmit the same pressure to the other pistons (B C D), which will move outwardly, unless they are each subjected to an equal and

Fig. 117.



Apparatus to demonstrate the equality of pressure in all directions.

opposite pressure (P). It is evident, therefore, that the pressure (P) exerted upon A is not only transmitted in a straight line upon B, but equally upon C and D—that is, equally in all directions. If now the axes of the jets B C D be disposed parallel to each other, and made to approach until they form one, and for the three pistons a single one be substituted, as in Fig. 119, the conditions of the pressure are in nowise changed, but it becomes at once evident that the pressure exerted upon the piston A, and transmitted by the fluid, is proportional to both the number and area of the pistons, whether existing separately as B, C, and D, or combined as B C D. That is to say, if a weight of one pound be placed upon the piston A, the three pistons B, C, D, or the one piston B C D, will be pressed outward by the pressure transmitted through the liquid, unless a weight of one pound be placed upon each of the pistons B, C, or D, or of three pounds upon the piston B C D. Suppose, however, that the apparatus be constructed of the form represented

Fig. 118.

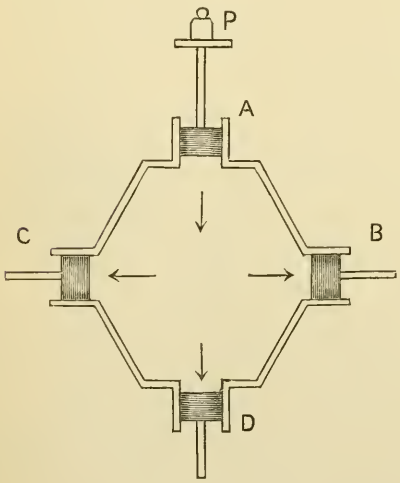
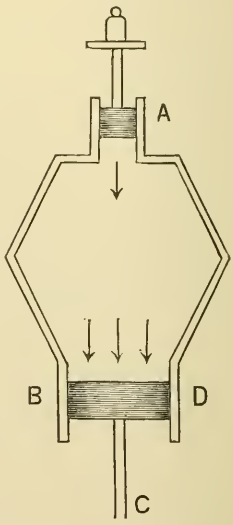


Fig. 119.



Apparatus to demonstrate pressure.

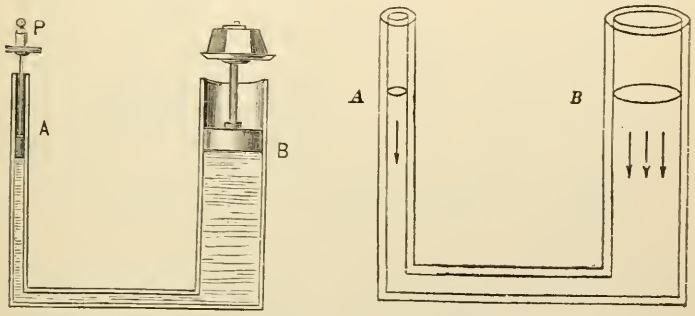
in Fig. 120, in which, as before, the large piston B has three times the area of the small one A, and carries three times as heavy a weight, it will be observed that while the small piston A with a weight of one pound and an area of one inch descends through three inches, the large piston B, with an area of three inches, and with a weight of three pounds, ascends through only one inch, equilibrium being then established, just as a lever whose arms have a length respectively of three and one inches will be balanced by suspending a one-pound weight at the end of the long arm, and a three-pound weight at the end of the short one. It is perfectly evident

that in neither case is there any absolute gain of power, for what is gained in weight is lost in height or distance.

In practical mechanics the Bramah press is a beautiful application of the principle just enunciated, in which a pressure of 300 pounds exerted upon a piston corresponding to A will exert a pressure of 30,000 pounds upon a piston B C D, supposing the sectional area of the latter to be 100 times that of the former. It must not be forgotten, however, that in the Bramah press, as in the simple apparatus just described, and in the case of the lever with unequal arms, that the greater weight is elevated only a fractional part of the distance through which the lesser weight has descended, and that what is, therefore, gained in weight is lost in distance. The significance of this important truth in the study of blood pressure will very soon become evident.

Now, on reflection, it will become evident from what has just been said with reference to the transmission of pressure through fluids, that the pressure exerted by the particles of water against each other must be estimated in exactly the same manner as we have estimated the pressure P transmitted to the base of the piston B (Fig. 120). It follows, therefore, that if the weights and pistons be removed from the apparatus (Fig. 120), that the water will rise to the same level in both of its limbs (Fig. 121), proving that the pressure exerted by the water in A and B must be equal and opposite, notwithstanding that the limb B contains three times as

FIG. 120. FIG. 121.

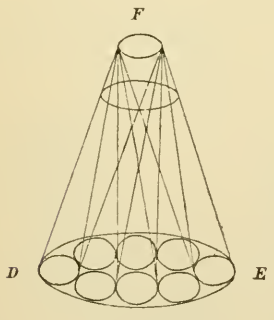


Principle of the hydraulic press.

much water as the limb A, for if the pressure exerted by the water in B were greater than that in A the level of the water would rise higher in the latter than in the former. It follows, therefore, from the principle of Pascal, or the equality of pressure, that the pressure exerted by a fluid is independent of the quantity of the fluid, and of the form of the vessel containing it, but is dependent for the same fluid on the area of the base upon which the pressure is exerted, and the height of the column of liquid above it. For let us suppose that the vessel, whose liquid contents

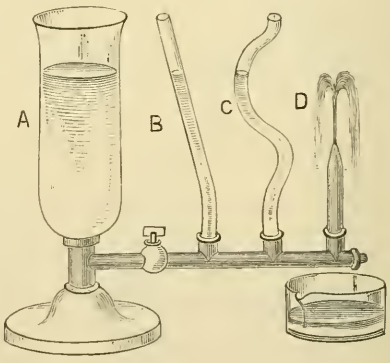
press upon the bottom, be of a tapering form, such as is represented in Fig. 122, and that the bottom D E be divided into eight areas of a size, equal to that of the mouth F. From what has been said of the pressure being transmitted equally in all directions, it follows that the weight of a small liquid layer, say half an inch thick at the top, will be transmitted undiminished to the eight areas of the bottom, producing the same pressure as if eight of such layers of liquid were separately placed upon them. In the same manner, a layer half an inch thick, but situated as much lower down in the liquid, so as to have twice the area of F, will produce the same pressure upon the bottom as if four such liquid layers were laid there—that is, the same as the pressure due to the eight small layers. It follows, therefore, that each horizontal layer of the same thickness, no matter where it lies in the liquid, produces the same pressure, the amount depending upon its thickness and the area of its base. The total pressure of the liquid upon the bottom must depend, therefore, on the area of the base, and its vertical height or thickness—that is, equal to a column of liquid having the same base and the same vertical height. The truth of the theo-

Fig. 122.



To illustrate the pressure exerted by liquids.

Fig. 123.



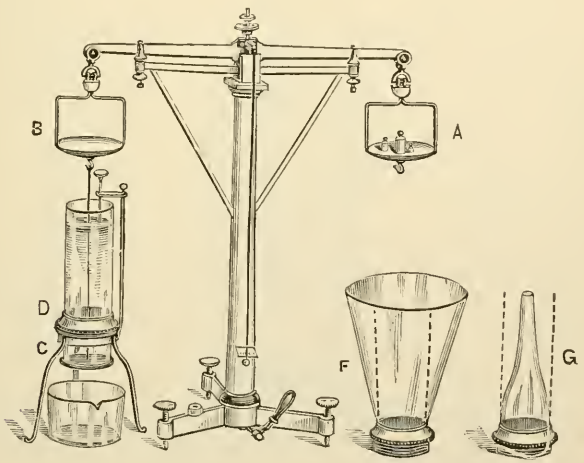
Apparatus to demonstrate that the pressure is independent of shape and size of vessel.

rem so deduced is experimentally verified by the experiment just performed, since the pressure exerted by the columns of liquid in A and B (Fig. 121) are the same, because they have the same base and the same height of liquid above it. That the shape of the vessel has no more influence with regard to the pressure exerted by the water it contains than that exerted by the amount will become, perhaps, more evident if the apparatus (Fig. 123) be filled with water. The level to which the water rises being the same in all the tubes, though of very different shape, proves that the pressure exerted by the water must be the same in all of them. On account, however, of the practical importance of the law of the pressure of liquids, and of the necessity of keeping clear in the mind the dis-

tinction between the pressure exerted by the liquid and its weight, let us illustrate the principle involved a little more in detail by means of the apparatus represented in Fig. 124.

This consists of a balance, in one of whose scale pans (A) a known weight is placed, while to the other (B) a wire is attached, terminating in a flat disk (C), which is so exactly applied to the lower opening of the supporting cylinder (D) that it practically constitutes its bottom, being tightly drawn up by the counterpoising weight in A. A known weight being now added to that already in A, and water being gradually poured into the cylinder, by degrees the pressure of the liquid on the disk or bottom increases, and when the pressure so exerted equals the counterpoising weight in A the least excess of water detaches the disk—that is, the bottom of the cylinder falls out, and the water flows out; but, as the pressure is at once diminished by the outflow, the disk is drawn up again and adheres closely to the cylinder. The pointer touching the surface of the water marks its level at the moment of equilibrium.

Fig. 124.



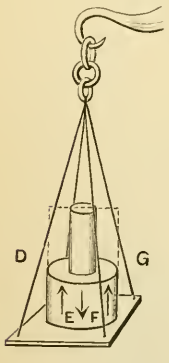
Pressure of a liquid on the bottom of the vessel which contains it.

In this experiment it is obvious, as might have been expected, that the pressure exerted by the water upon the bottom is precisely equal to its weight, which was two pounds. Suppose, now, we substitute for the cylinder a conical-shaped vessel (F), with the same sized orifice at the bottom, but with a much wider one at the top, and, therefore, capable of containing more water; nevertheless, if we experiment with the conical vessel as we did before with the cylinder, notwithstanding that the former contains three times as much water as the latter, the pressure exerted by the water upon the bottom, as we see, is the same, being only two pounds, whereas the water weighs six pounds. In the experiment with the conical

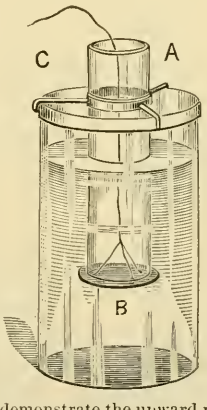
vessel the pressure exerted by the water upon the bottom is, therefore, less than its weight, and the reason is very obvious, since it is only that part of the water within the dotted lines that exerts pressure upon the bottom, the pressure of the remaining extra water, so to speak, being exerted upon the walls of the vessel, and not upon its bottom.

Finally, if we make use of a conical vessel (Fig. 124, G), or of one (Fig. 125) consisting of two cylindrical parts of unequal diameters, of which the lower one has the same sized orifice at the bottom as obtains in the two vessels just used, and holding less water than either of the latter, we shall still find, experimentally, in the same way, that the pressure exerted upon the bottom is undiminished by that circumstance, being two pounds, though the water weighs only one pound. This must be so, since the pressure exerted upon the bottom is due to a column of water having the same vertical height and base as the column of water included between the two dotted lines D and G (Fig. 125)—that is, the pres-

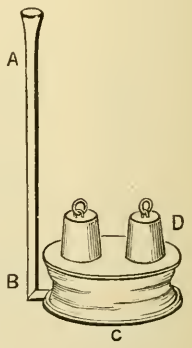
Fig. 125. Fig. 126. Fig. 127.



Hydrostatic paradox.



To demonstrate the upward pressure exerted by water.



Hydrostatic bellows.

sure of the column of water on the principle of the pressure being exerted equally, and in all directions, is not only exerted upon E F (Fig. 125), or the part of the bottom directly underneath it, but also upon the remaining part of the bottom on both sides of E and F. The total pressure exerted upon the bottom is, therefore, the same as if there were two extra columns of water (D, G) pressing downward in addition to that upon E F actually present. It will be observed in this experiment that the pressure exerted by the water upon the bottom is, therefore, greater than its weight. At first sight, this result may appear paradoxical, it being perhaps difficult to comprehend why, if the water in the vessel exerts a pressure upon the bottom, that when the vessel is placed in the scale-pan of the balance that its weight should be only equal to the

weight of the water and vessel. The reason, however, becomes at once clear when it is remembered that the pressure of the water is exerted in all directions, upward as well as downward, and that when the vessel is placed in the scale-pan (Fig. 125), that part of the pressure exerted upward against the surface of the vessel in the direction of the arrows, being opposed in direction to the force of gravity, does not appear as weight; consequently, the weight is simply equal to the weight of the vessel and of the water it contains. If, however, this upward pressure be balanced by an equal downward pressure, obtained by an extra quantity of water, equal in amount to the volume included between the dotted lines, then the pressure and weight of the water would be identical—that is, the conditions would be the same as in the first experiment.

That the pressure of the water is transmitted upward as well as downward can be readily demonstrated by the following simple experiment. A large open glass tube (A, Fig. 126), one end of which is ground, is fitted with a thin card (B), to the center of which is attached a string (C) by which it can be held against the bottom of the tube. The whole is then immersed in a jar of water, and, although the string be allowed to hang over the side of the jar, the card will still adhere to the mouth of the jar, it being kept in this position by the upward pressure of the water.

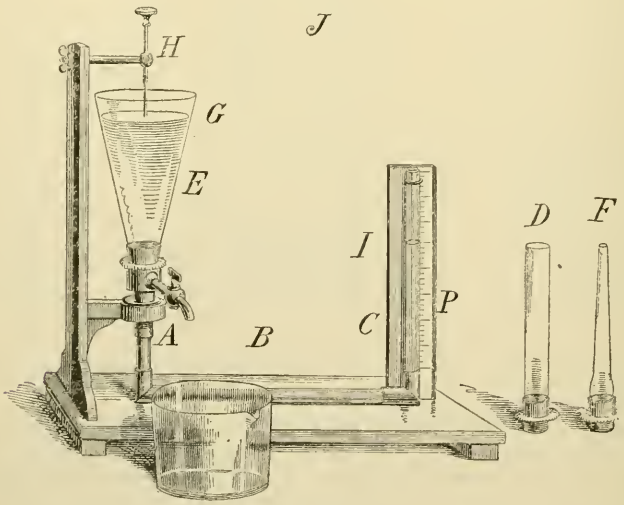
If now water be slowly poured into the tube the disk will still adhere to the latter, not sinking until the height of the water inside the tube is equal to the height outside. Hence it follows that the upward pressure is equal to a column of water whose area is that of the tube (A), and whose height is the distance from the disk to the outer surface of the liquid. The upward pressure is, therefore, governed by the same law as the downward pressure.

The hydrostatic bellows (Fig. 127) is an interesting instrument in this connection, as illustrating the principle of Pascal, and the manner in which we propose to study blood pressure. It consists of a narrow tube (A) eight feet in length, with a sectional area of one-fourth of an inch, inserted into a square bellows (C) having a superficial area of one hundred and forty-four inches. The apparatus having been filled with water, it follows that, as the water in the tube weighs fourteen ounces, and as the superficial area of the top of the bellows (144 inches) is 576 times that of the sectional area of the tube (one-fourth of an inch), the bellows (D, D) should balance a weight of fourteen ounces multiplied by 576, equals 8064 ounces, equals 504 pounds, which, as a matter of fact, it does. At first sight this result may appear as paradoxical as in the experiment with the cylindrical vessel; it will be observed, however, that the distance through which the 504 pounds upon the bellows are elevated is but the one-sixth of an inch, a fractional part only of the ninety-six inches through which the pressure was exerted. It is only another illustration of what we gained in weight we lost in height, or of a small force acting through a great height being equal

to a large force acting through a short one, fourteen ounces falling through ninety-six inches, being equal to 8064 ounces, or 504 pounds, ascending through the one-sixth of an inch. It follows, therefore, that the pressure even of a small quantity of water, if exerted from a sufficient height, will be very great; indeed, Pascal succeeded in bursting a strongly made cask by means of a narrow thread of water forty feet high, and, in this manner, demonstrated his principle of the equality of pressure.

In considering the pressure exerted by two columns of liquid such as obtains in the apparatus (Fig. 121), it will be remembered that only one liquid—water—was used. It is needless to say, however, that if two liquids of different densities, such as water and mercury, were experimented with, the level of the water would stand 13.5 times higher than that of the mercury, the latter being that much heavier, the altitudes of the liquids being inversely as their densities. In other respects, what has been said of the pressure exerted by water will apply equally to mercury or other liquids, and inasmuch as we will make use of a mercurial column as a measure of the pressure exerted by the blood, it will not be superfluous to illustrate first the manner in which we measure by mercury the pressure exerted by any liquid; this we do by means of

FIG. 128.



Haldat's apparatus.

Haldat's apparatus (Fig. 128). This consists of a tube (*A B C*) bent at both ends at right angles, one of which is provided with a stopcock (*A*) on which can be screwed vessels (*D, E, F*, etc.), of the same height, but differing in shape and capacity. The tube *A B C* is filled with mercury until it reaches the level *P*. The vessel *E* is first screwed on, for example, to the end at *A* and water

is poured into it until it reaches the level *G*, this level is registered by the movable rod *H*. The pressure of the water in the vessel *E* upon the surface of the mercury in the limb *A* will cause the mercury to rise in the tube *C* up to the level *I*, and is there registered by a movable collar.. The stopcock *A* is then opened, which allows the water to run out of the vessel *E*, which is then removed and is replaced by the vessels *D* and *F*; these, in turn, are filled with water up to the level *G*, when it will be observed that the mercury which had in the meantime, in each case, fallen to its original level in limb *A*, rises again to the level *I* the same as before, thus proving that the pressure exerted by the water upon the mercury is, as we have already seen, independent of the quantity of the water and of the shape of the vessel, but is equal to the weight of a column of water whose base is the surface of the mercury *M* beneath the stopcock in limb *A*, and whose altitude is the height (*A G*) of the level of the water above the surface of the mercury, that is, the pressure of the water (*P*) equals altitude (*A G*) multiplied by area (*M*). The height of the water being the same in *D F* and *E*, and the surface of the mercury (*M*) representing the area in each case, the product of *A G* × *M* must give the pressure exerted by the water in all three vessels, which we have just seen is the case, the column of mercury being the same in both experiments.

The column of mercury is then the measure of the pressure exerted by the water in *D*, *F*, or *G* sustaining it. It is obvious that we must double *P I* as the mercury is proportionally depressed in the other limit of the tube. It is by means of the hydrostatic principles that we have illustrated somewhat in detail that Stephen Hales, in the early part of the last century, first determined the cardiac blood pressure in a living animal with anything like accuracy, and estimated what it would probably be in man. Hales's method[1] of experimenting was as follows: A living animal, a horse, for example, having been firmly secured, a large artery, like the femoral or carotid, was exposed, and, after having been ligated, was opened. A brass tube was then inserted into the vessel, to which was adapted a glass tube ten feet long. The connection between the brass and the glass tube was made by a brass pipe, and in some cases by a portion of the trachea of a goose, the latter being used on account of its pliancy so that no disarrangement would ensue through the struggles of the animal. The tube having been inserted into the femoral artery, for example, the blood was observed to rise in the glass eight feet three inches above the level of the left ventricle of the heart. In the case of the carotid artery the blood rose even higher, attaining a height of nine feet six inches, or 114 inches. In order to estimate the pressure or force sustaining such a column of blood, just as in the case of the experiment with the water and the mercury, or with the bellows, the altitude, 114 cubic inches, must be multiplied by the internal surface of the left ventri-

[1] Statical Essays, Vol. ii., pp. 1, 2, 14, 15, 19, 20, 21, 39, 40. London, 1740.

cle of the horse's heart, or the area. Hales determined the area of the left ventricle of the horse's heart by injecting it with hot wax, then the wax, when cold, was removed and small pieces of paper properly cut were placed upon it until the wax was perfectly covered; the small pieces of paper were then removed to a sheet of paper which was ruled off into squares, and in this way it was estimated that the inner surface of the ventricle, or the area needed for the calculation, was equal to 26 inches, deducting 1 inch for the orifice of the aorta. The pressure or the force of the liquid, in this case the blood in the carotid artery, being independent of the quantity and the shape of the vessel containing it, but equal to the altitude of the column of the blood multiplied by the area or its base, the product of 114 inches by 26—that is, 2,964 inches of blood—will be the pressure or force which the ventricle sustains at the moment of its systole. Now, as a cubic inch of blood weighs 267.7 grains, the pressure of the blood amounts to 267.7×2964, or 793462.8 grains, which is a little over 113 pounds, there being 7,000 grains to the pound. On the supposition that the blood would rise $7\frac{1}{2}$ feet high in a tube inserted into the carotid artery of a man, and that the internal area of the left human ventricle is equal to 15 square inches, Hales estimated by the method just mentioned, that the pressure on the left ventricle at the moment of contraction would amount to 51.2 pounds. This estimate is too low, as the later investigations of Poisseuille, Volkmann, etc., to be described presently, have shown that the blood would probably rise in a tube placed in a carotid artery of a man as high as in that of the horse, there being but little difference probably in this respect as regards these mammals. Indeed, Volkmann[1] has demonstrated that even in the chicken the blood rises as high in some instances as in the dog and the horse. Further, Haughton,[2] by a different method from that of Hales, calculated that the cardiac blood pressure in man ought to be about the same as that observed in the horse, his method being based upon a knowledge of the distance to which a divided artery will spurt, which in the case of man was learned by Haughton through a surgical operation, the force with which the heart contracts to produce such an effect being deduced from his data.

Modern investigation, as we shall see, has shown that the blood pressure is influenced by conditions unknown to Hales, nevertheless his original experiment is to this day the most striking way of demonstrating it, and his application of hydrostatical principles in measuring it is the method since so successfully made use of by Poisseuille, Volkmann, Ludwig, and others.

It is not so much, however, the pressure that the heart sustains which the physiologist wishes to determine as the actual force with which the heart drives the blood into the aorta at each ventricular

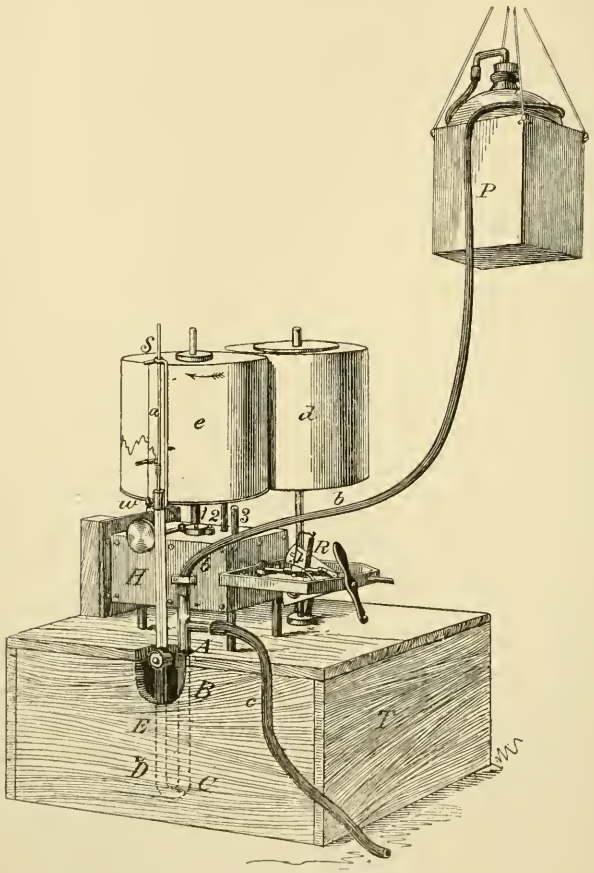
[1] Die Hæmodynamik, s. 177.
[2] Animal Mechanics, p. 40. London, 1873.

systole. The difference between the action of the heart and that of the hydrostatic apparatus we have shown, in which the large glass tube and bellows represent the aorta and heart, is that the heart, like any other muscle, exerts itself according to the resistance to be overcome. Thus, if we raise a pound with our hand, the muscles of the extremity make a greater effort than when we raise a feather, so according to the resistance, for example, offered by the capillaries to the efflux of the blood into them from the arteries, will the heart contract more forcibly, and the blood-pressure will rise. It is evident, then, that the possible force of the heart and the actual force usually exerted may differ very much in amount. Before demonstrating this experimentally let us describe the hæmodynamometer, the apparatus by means of which blood pressure is usually studied at the present day, and then compare the arterial with the cardiac pressure. The hæmodynamometer, so called from the Greek words *αἷμα*, blood, *δύναμις*, power, and *μετρον*, measure, is essentially a mercurial manometer adapted to measure the blood pressure, hence the name given to the instrument by Poisseuille,[1] who first, in 1828, made use of it for this purpose. The apparatus that we shall use (Fig. 129) is the same as Poisseuille's, with some modifications. It consists of a U-shaped glass tube (B C D E), of which the distal or ascending limb (D E) is longer than the proximal or descending one (B C). From the proximal branch B is given off a short horizontal one A, by means of which the manometer is put in communication with the artery whose blood pressure we wish to determine, and which, in this case, will be the carotid artery of the rabbit. The U-shaped tube being clamped in a vertical position, perfectly clean and dry mercury is poured into it until the mercury reaches a given level in the two limbs. To prevent the blood coagulating that which will come from the artery a saturated solution of sodium carbonate is allowed to flow from the pressure-bottle P through the tube *b b* into the proximal end B of the manometer, and through its horizontal branch (A), to which is connected by a short piece of tubing a glass tube, or leaden pipe (*c*), the latter being stopped temporarily by the finger, or by a cork. To avoid the inconvenience of inserting the horizontal branch of the manometer A, or its continuation the pipe *c*, into the artery, and which would be impossible in the case of the rabbit, the vessel being so small, a pointed and bevelled glass canula is first inserted into the artery, the vessel having been previously ligated at its distal end, and clamped at its proximal end. The insertion of the canula will be greatly facilitated if a small piece of card be placed under the vessel to support it, and by making the opening for the canula V-shaped. The canula is secured in the artery by a ligature, and is connected with the pipe *c* by a small piece of tubing. The arterial canula is filled with the solution of sodium bicarbonate by means of a syringe, and the same solution

[1] Journal de physiologie de Magendie, Tome viii., p. 272, 1828.

allowed for a moment to flow from the pressure-bottle into the proximal limb of the manometer, and through its horizontal branch and the pipe *c*, so that all the air shall be driven out. The arterial canula and the pipe *c* are then connected as quickly as possible, and the tube (*b b*) leading from the pressure-bottle to the proximal limb

FIG. 129.



The mercurial kymograph. *a*. Vulcanite rod of floating piston. *b*. Tube which communicates with the pressure bottle. *c*. Tube which communicates with the artery. *d*. Feeding cylinder. 1. First axis, which revolves once in a minute. 2. Second axis, which revolves once in ten seconds. 3. Third axis, in a second and a half. The instrument is furnished with other cylinders suitable for the reception of single bands of glazed paper, the surface of which can be blackened after they are fixed on to the cylinders, by causing the latter to revolve over the flame of a petroleum lamp.

of the manometer clamped. On removing the clamp from the artery the blood will jet out, pressing forward against the soda solution, which, in turn, will press against the mercury in the proximal end of the manometer, forcing it downward, the mercury in the distal limb being proportionally elevated, and which having reached a

certain level will then oscillate above and below the same with each beat of the heart. It will be observed that during the systole the force of the heart not only expends itself in elevating the column of mercury, but also in distending the walls of the artery. The effect of the latter is that during the diastole through the elastic recoil of the arterial walls the mercurial column is kept elevated, though not as high as during the systole. It may be mentioned incidentally in this connection, that the pressure due to the elastic recoil of the walls of the artery is usually designated arterial pressure, as distinguished from the direct pressure due to the contraction of the heart and known as cardiac pressure. It must be borne in mind, however, in making this distinction between arterial and cardiac pressure that the former is only the delayed effect of the latter, since the cardiac pressure exerted during the systole in distending the arterial walls is restored during the diastole as the elastic recoil of those walls or the arterial pressure. It is evident from the hydrostatical principles just illustrated that the pressure of the blood in the artery will be measured by the weight of the column of mercury, whose base or area is a circle, having the same diameter as that of the artery, and whose altitude is the height of the column of mercury—that is, the difference between the two levels F and G, and which, in this particular experiment, it will be observed, amounts to 90 millimeters (3.6 inches). The arterial pressure can be briefly and conveniently expressed then by the formula P equals $\pi R^2 h W$, in which P equals the pressure, πR^2 the area of the artery, h, the height of the mercury, and W its weight, it being understood that the symbol π is the ratio of the circumference to the diameter, and R^2 the square of the radius of the circumference of the artery, and that the product of π by R^2 gives the area.

To illustrate the manner in which this formula can be made use of let us determine, at least approximately, by its means the pressure exerted by the blood upon the semilunar valves of the aorta in man. Let us assume [1] that the diameter of the aorta at the level of the semilunar valves in a man aged twenty-nine years was 34 millimeters. The radius R being 17 millimeters, and its square 289 millimeters, the area of the aorta would be equal to 289 millimeters multiplied by 3.1416 (π) or 907.9 millimeters. The latter or the area being multiplied by 200 the probable height to which the mercury would be elevated in millimeters, could the manometer tube be inserted into the human aorta, gives 181580 millimeters, or 2453 grammes (one cubic millimeter of mercury weighing $\frac{1}{7\frac{1}{4}}$ of a gramme) as the pressure sustained by the aortic valves in man. Or, more briefly, by substituting in the general formula the particular values

$$P = R^2 \times \pi \times h \times W$$

$$\text{Pressure} = 289 \times 3.14 \times 200 \times \tfrac{1}{7\frac{1}{4}} \text{ gramme} = 2.453 \text{ kilogrammes}$$

[1] Poisseuille, op. cit., p. 304.

It may be said then that the actual pressure under which the blood is driven into the aorta at each ventricular systole may amount to 2.4 kilogrammes (5.2 pounds). As a general rule, however, the blood pressure is estimated by simply measuring the height to which the mercury is elevated in the distal limb of the manometer, and doubling the result, without the area of the artery or the weight of the mercury being taken into consideration. By that method the aortic pressure would be estimated as amounting to 200 millimeters.

The disadvantage of such a manner of estimating blood pressure is due to the fact already mentioned that the difference between animals as regards the height to which the mercury will rise in the manometer is not as great as perhaps might have been at first imagined. Since the blood pressure depends not only on the height of the mercury in the manometer, but also on the area of the artery, we should expect to find, as indeed is the case, that while the height of the mercury is about the same in different species of animals, that the blood pressure may be absolutely very different, though relatively the same per unit of area. As the aortic blood pressure is equal to the height of the mercurial column multiplied by the area of the aortic orifice it is evident that the pressure will be proportional to the size of this orifice, and will, therefore, be greatest, other things equal, in that animal which has the largest aorta. Thus the aortic blood pressure of man as estimated simply in millimeters of mercury differs but little from that of the horse; on the other hand, the aortic pressure in the horse, as estimated in the above manner, is greater than that in man.

In estimating blood pressure a fact must be taken into consideration which is usually neglected, and that is, that the solution of sodium carbonate having weight must exert a certain amount of pressure upon the mercury in the manometer. The height to which the mercury is elevated is then due to the pressure of the blood and of the solution. To obtain the former we must therefore deduct the latter from the observed altitude of the mercury. As 10 millimeters ($\frac{2}{5}$ in.) of the soda solution are equal to 1 mm. of mercury for every 10 mm. of the soda solution in the proximal limb of the manometer we must deduct then 1 mm. of mercury from the altitude of the mercury in the distal limb of the manometer. As a general rule, the amount of the soda solution in the proximal limb of the manometer is so small that the effect of its weight upon the mercury need not be considered. Thus, in determining the blood pressure in the carotid artery of the rabbit it will be noticed that the solution of soda amounts to only 5 mm. ($\frac{1}{5}$ in.), and therefore only $\frac{1}{2}$ mm. must be subtracted from the 90 mm., or the observed altitude of the column of mercury, to obtain the arterial pressure. In using certain kinds of manometer, however, as we shall see, the amount of the soda solution being greater the influence of its pressure becomes more appreciable. It will be observed, also, that the pressure bottle containing the solution of sodium carbonate is sus-

pended at a height of about 2 meters (6.4 feet) above the manometer, and that it can be elevated or depressed as desirable. The object of this is that having learned by experience to about what height the mercury will be elevated by the arterial pressure, we make use of the soda solution not only to prevent the coagulation of the blood, but also to exert pressure upon the mercury to the same extent as the arterial blood will do. As soon as the clamp is removed from the carotid artery the blood at once then exerts its pressure upon the soda solution, but advances only a little way in the tube *c* (Fig. 129), loss of blood as well as coagulation being thereby prevented. The pressure of the blood is then transmitted to the soda and thence to the mercury; if the pressure bottle has not been sufficiently elevated, then the level of the mercury will rise in the distal limb of the manometer, and if too much elevated the reverse will be the case. The effect of the arterial pressure will therefore be the same as if exerted directly upon the mercury.

In speaking of the connecting tube *c* (Fig. 129), it was mentioned that it should be of glass and preferably of lead. The reason of this is now very evident. Did the tube consist of an extensible material the pressure of the blood would be exerted to a great extent upon the walls of the tube rather than upon the soda solution, and therefore not upon the mercury.

We have just seen that the pressure of the blood upon the aortic valves in man may amount to 2.4 kilogrammes (5.2 lbs.). Now, since the pressure exerted upon the mass of a liquid is transmitted undiminished equally and in all directions and acts with the same force upon all equal surfaces, according to the principle of Pascal to obtain the cardiac pressure we have only to multiply the aortic pressure (2.4 kilogrammes) by the ratio of the aortic area (907.9 millimeters) to the internal area of the left ventricle (100 square centimeters), which gives

$$2.4 \text{ kilogrammes} \times \frac{100}{9.079} = 26.4 \text{ kilogrammes} = 58 \text{ pounds} = \text{cardiac pressure}$$

This estimate of cardiac pressure is, of course, somewhat greater than that obtained by Hales (51.2 pounds), since the latter assumed that the blood would be elevated 7.5 feet (175 mm. of mercury), instead of 8.5 feet (200 mm. of mercury).

If, now, the hydrostatic bellows (Fig. 127) be compared with the heart and aorta, it is obvious that the small force acting through a great height in the narrow tube, corresponds to the aortic pressure, and the great force acting through the small height in the bellows, corresponds to the cardiac pressure.

A great advance was made by Ludwig,[1] in 1848, in the manner of investigating blood pressure, by his invention of the kymograph (Fig. 129). This consists of a mercurial manometer like that of Poisseuille, in the distal limb of which is placed a vertical rod (*a*),

[1] Müller's Archiv, 1847, s. 242.

the lever-end of which terminates in a concave cup-shaped float, and rests upon the convex surface of the mercury, while the upper end of the vertical rod projects out of the upper open end of the distal limb of the manometer, and carries a delicate sable brush, wetted with ink, or a pen of glass, the point of which rests against the cylinder *c*. The vertical rod is kept in the perpendicular by the support *s*, through which it passes, and the brush or pen in contact with the cylinder by the weighted string *o*. The cylinder *c* is covered with either white or smoked paper. With every oscillation of the mercury in the distal limb of the manometer, the rod *a* is elevated or depressed, and a vertical line is made upon the cylinder by the brush or pen. If now the cylinder is made to revolve at a uniform rate, the vertical mark will become a curve, like that represented in Fig. 130, and we obtain a graphic representation of the

Fig. 130.

Trace of blood pressure in rabbit.

blood pressure, hence the name kymograph given to the instrument —from *κυμα*, a wave, and *γραφω*, to write. It may be mentioned that the idea of the recording pen, etc., was suggested to Ludwig by a similar contrivance made use of by Watt for registering pressure in the steam engine. The immense importance of Ludwig's invention cannot be exaggerated, for, by means of the kymograph, the study of blood pressure became far more exact than had been possible previously.

Slight variations in the oscillation of the mercury, for example, which were entirely inappreciable in the hæmadynometer, became perfectly apparent when graphically recorded upon the revolving cylinder. The great merit of Ludwig's invention did not consist simply in the application of the kymograph to the study of the blood pressure, but the application of the graphic method in the investigation of the circulation of the blood generally, and indeed, of all physiological phenomena. In truth, it is not saying too much that the study of physiology experimentally has been revolutionized by it, results having been obtained by the graphic method, as we have already seen, which had been considered impossible by the physiologists of the preceding generation.

As the mercurial manometer of the kymograph, with its accessories, the pressure bottle, connecting tubes, etc., is the same as that already described, it is only necessary to say that the mercurial manometer, when used as part of the kymograph, is firmly clamped to the table (*T*, Fig. 129) supporting the cylinders, the latter being moved by clock-work contained in the box *H*, and the motion made uniform by the Foucault regulator (*R*). This consists of two fans, which, when the velocity is increased through the frie-

tion engendered, expand and so retard the motion, and when the velocity diminishes contract again, and so offering less resistance it increases again, the fans being approximated and separated by an elastic spring. There are three axes (1, 2, 3) connected with the clock-work, and according to the one on which the cylinder is placed the rate of its revolution can be varied.

When the cylinder used is that covered with smoked paper, it is held on the axis connected with the clock-work by a vertical rod passing from its center upward into the frame, and which is screwed on to the box. By means of this vertical rod the cylinder can also be elevated or depressed through a height of several centimeters. When, however, a trace is taken upon white paper, and it is desirable that the observation shall extend over as long a period of time as possible, then a somewhat different arrangement is made from that just described. Two cylinders are then used (Fig. 129, *c*, *d*), one of which (*c*) is to record the trace, and which, resting upon the axis connected with the clock-work, is supported from above by a frame, not represented in the figure, which, like the other frame, can also be screwed on to the box. The other cylinder (*e*) is covered with white paper rolled around it by machinery, and in quantity sufficient to last for several hundred observations. This cylinder acts as a feeder to the recording one, for, as the latter revolves, it unwinds the white paper around the former, the paper being kept smooth by two little ivory wheels on the frame (not represented in Fig. 129). Having explained the construction of the kymograph, let us consider now the traces of blood pressure of the cat, turtle, frog, for example, as recorded by it, and point out some of the results obtained by their study, and which would have been impossible had the study of blood pressure been limited to the use of the mercurial manometer only. By an examination of Fig. 131, illustrating the kymographic trace of the blood pressure in the cat, recorded upon the smoked paper, and preserved by varnishing, it will be observed that the trace consists of a number of large curves,

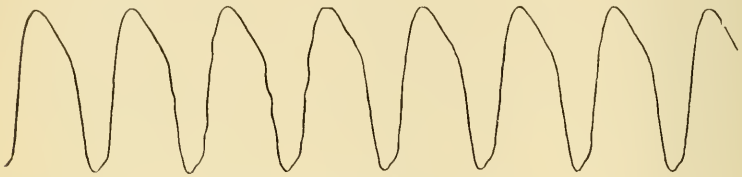
FIG. 131.

Trace of blood pressure in cat.

each of which is made up of smaller ones. The large curves extending from crest to crest of the wave, being to a certain extent respiratory in origin, their relations to inspiration and expiration will be considered hereafter. For the present, however, it may be said that during a part of the period of inspiration the blood pressure is increased and during a part diminished, and that in the same way the blood pressure is both diminished and increased during expiration.

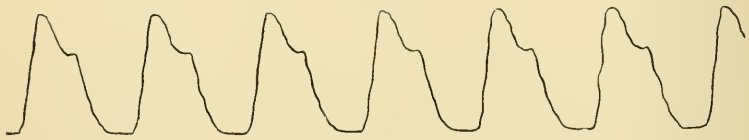
As respiration is far less active in the turtle and frog than in the rabbit, it will be seen, as might have been expected, that respiration does not influence in these animals, to any great extent, the form of the curve of blood pressure. Indeed, the respiratory curves are absent in the traces of the blood pressure of the turtle and frog (Figs. 132, 133), the curves in the latter traces being cardiac in origin and corresponding to the small curves of Fig. 131.

Fig. 132.



Trace of blood pressure in turtle.

Fig. 133.



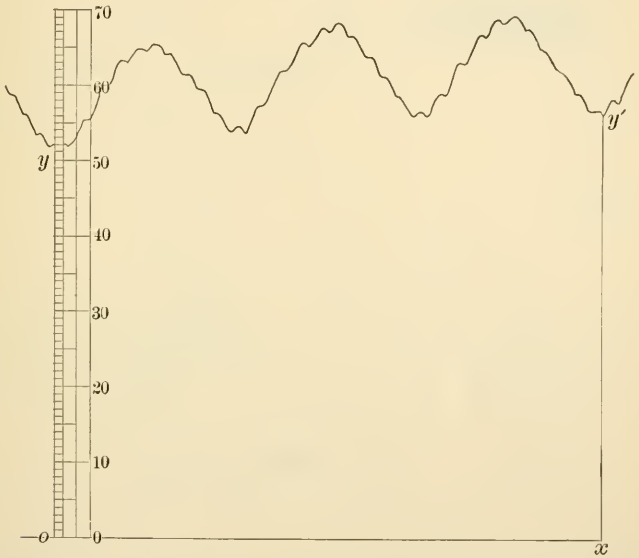
Trace of blood pressure in frog.

The small curves in the mammal being cardiac in origin, each small curve corresponds to a heart-beat, the elevation being caused by the systole, the depression by the diastole. If the pen be watched during these oscillations, it will be noticed that there is an average height above and below which the pen is elevated and depressed with each cardiac beat. This average height represents the mean cardiac pressure. On the other hand, the average vertical distance or ordinate between the horizontal line or abscissa, representing the height at which the pen is sustained by atmospheric pressure only, and the horizontal line representing the height at which the pen is sustained through the elastic recoil of the arterial walls, represents the mean arterial pressure. To obtain either the mean cardiac or mean arterial pressures the respective ordinates must be added and the sum divided by the number of ordinates and the quotient multiplied by two. The cardiac or arterial pressure, however is determined at any one moment in millimeters of mercury by simply observing the difference between the levels of the mercury in the proximal and distal limbs of the manometer. Very great differences are found, also, among animals, as regards the proportion of the cardiac to the arterial pressures. In the rabbit, for example, the force of the left ventricle exceeds but little that of the aorta, whereas, in the horse, the excess of the cardiac pressure as compared with the arterial is very marked. Thus, by means of his

cardiometer, Bernard[1] has shown that the arterial pressure in the rabbit, being 95 mm. (3.8 inches), with each ventricular systole the mercury rose to 100 mm. (4 inches), the cardiac pressure being only 5 mm. greater than the arterial. On the other hand, in the horse, the arterial pressure being 110 mm. (4.4 inches), the cardiac pressure was 65 mm. greater, the mercury rising to 175 mm. (7 inches) with the systole.

Just as we have seen the pulse gradually disappearing as we recede from the heart, so, for the same reason, we should expect to find this excess of cardiac over arterial pressure becoming less and

FIG. 134.



Blood-pressure curve of the carotid of a dog obtained with a mercurial manometer. o–x = line of no pressure, zero line, or abscissa; y–y' is the blood-pressure tracing with small waves, each one caused by a heart-beat, and the large waves due to the respiration. A millimeter scale shows the height of the pressure in millimeters of mercury. (LANDOIS.)

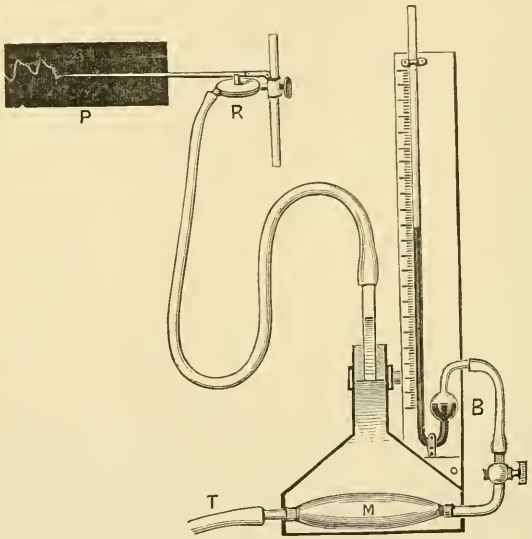
less as we pass toward the periphery. Experiment confirms in this respect what theory would lead us to expect. Thus, Volkmann[2] has shown that, while in the carotid artery of the dog the excess of the cardiac pressure, as compared with the arterial, amounts to 37 mm. (1.4 inches), in the metatarsal artery the excess amounts to only 1 mm. ($\frac{1}{25}$ of an inch).

The cardiometer, made use of in demonstrating the difference between cardiac and arterial pressure (Fig. 135), consists of a metallic vessel containing water, within which is suspended an elastic capsule (M), communicating at one end (T) with the artery whose pressure is to be determined, and at the other end with a delicate mer-

[1] Systeme Nerveux, Tome i., pp. 283, 286.
[2] Die Hæmodynamik, s. 167.

curial manometer (B) for registering the pressure. The upper part of the vessel is closed with a cork through which passes a glass tube, into which the water rises, and which transmits to the registering tambour R the distention of the capsule M due to the varying cardiac pressure. The arterial pressure, however, when once attained, remains constant, the constriction at the bottom of the mercurial manometer B offering such a resistance to the rise of the mercury that the intermittent action of the heart is not felt.

Fig. 135.



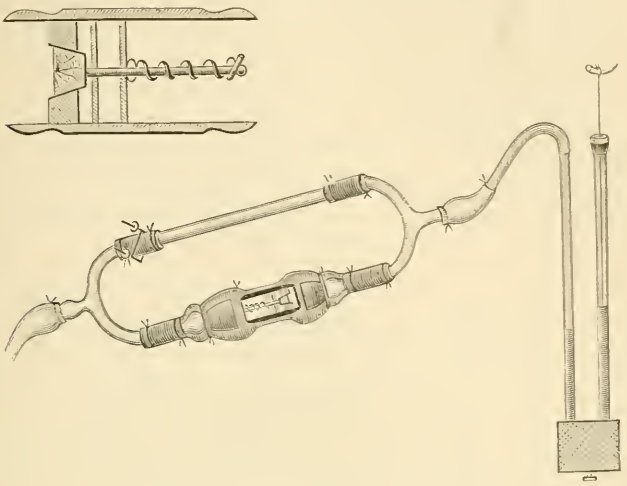
Cardiometer. (Marey.)

Not only does the cardiac vary in relation to the aortic pressure, but the cardiac pressure varies itself. Thus, it has been shown by means of the Goltz-Gaule manometer (Fig. 136) that there is in the dog, for example, a maximum and a minimum intra-ventricular pressure, amounting to 140 and –50 millimeters of mercury respectively.[1] The latter being a negative pressure that is lower than that of the atmosphere, the blood will be forced into the heart as we shall see more particularly hereafter. The instrument just referred to by which variations in the intra-ventricular pressure is usually determined, consists essentially (Fig. 135) of two parts, one of which (*a*) acts as an ordinary manometer, the other as a maximum or minimum manometer according to the position of the valve (*v*) the part (*a*) being then clamped. The valve (*v*) is of a cup and ball variety, and when, as in Fig. 138 permits the passage of the fluid from the heart, but not towards it. Since the

[1] Fr. Goltz u. J. Gaule, Pflüger's Archiv, Band xvii., 1878, s. 100; S. de Jager, Ebenda, Band xxx., 1883, s. 491.

column of fluid that passes the valve can not return, the mercury will remain at the greatest height to which it has been elevated,

FIG. 136.



The maximum manometer of Goltz and Gaule.

the instrument then acting as a maximum manometer. By reversing the valve the manometer is then converted into a minimum one.

Slight variations in the intra-auricular, ventricular, and aortic pressures can be much better demonstrated, however, by means of

FIG. 137.

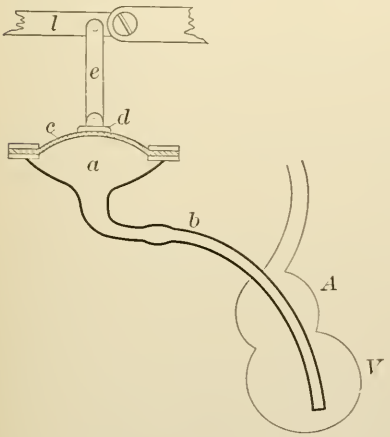
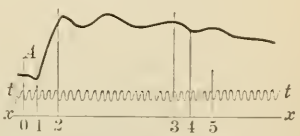


Diagram to illustrate the essential parts of Hürthle's membrane manometer.

FIG. 138 V.

Curve of pressure in the left ventricle of the dog, Hürthle's membrane manometer. (FOSTER.)

FIG. 138 A.



Curve of pressure in aorta of dog. (FOSTER.)

membrane manometers than mercurial ones, the inertia of the mercury in the latter being too great to be much affected. Among the

membrane manometers or tonometers, as they are also called, made use of for this purpose that of Hürthle[1] is a convenient form. This consists essentially of a very small metal hemispherical drum (Fig. 137, *a*), the upper end of which is covered with a delicate elastic membrane (*c*), bearing upon its center a thin metal disc (*d*), connected by a short upright (*e*) with a recording lever (*l*), the lower end terminating as a tube (*b*).

Fig. 139.

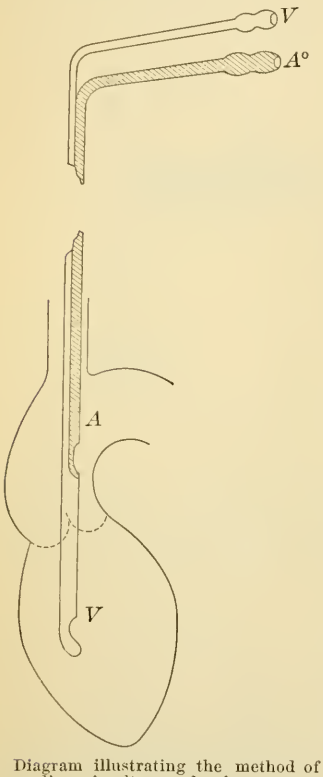


Diagram illustrating the method of recording simultaneously the pressure in the left ventricle and at the root of of the aorta. (Hürthle.)

A catheter filled with sodium carbonate solution having been introduced through the jugular vein into the right auricle (*A*) or ventricle (*V*), or through the carotid artery into the aorta, and so into the left ventricle, connection is made with the manometer, the latter being usually filled with the same solution as that in the catheter. Such being the disposition of the apparatus, it is obvious that any variations in the pressure exerted by the heart cavities will be transmitted through the fluid of the catheter and drum to the elastic membrane of the latter, and in turn transmitted thence to the recording lever. It will be observed that the curve (Fig. 138 *V*) of the pressure of the left ventricle in the dog obtained by the Hürthle manometer, as well as that of the right ventricle of the horse obtained by a Marey sound (Fig. 93), agree in the following features: the pressure rises at the very beginning of the systole very rapidly, soon reaches a maximum, which is maintained at nearly the same height for some time, that part of the curve constituting the "systolic plateau," then rapidly falls to the line of atmospheric pressure, or even below it, and remains at the base line till the next cardiac beat. It must be mentioned, however, in this connection, that, according to some observers, the production of the so-called "systolic plateau" is due to the friction of the tube, ill-placed canula, etc., the highest point of pressure being naturally peaked, not flattened. By introducing two catheters into the heart of a dog so that the end of one will lie in the ventricle (Fig. 139 *V*), the end of the other in the aorta (*A*), and then connecting the other ends of the catheters with two membrane manometers, the pressure of the ventricle and auricle can be simultaneously recorded.

[1] Pflüger's Archiv, Band xliii., 1888, s. 399.

An examination of the two curves (Figs. 138 V and 138 A) shows that at (o), Fig. 138 V, the beginning of the ventricular systole, no effect is produced upon the blood of the aorta, the latter being cut off from the influence of the ventricular pressure by the closing of the aortic valves. A little later, however, as at (1), Fig. 138 A, the aortic valves being now open the effect of the ventricular pressure is felt and the pressure in the aorta begins to rise. The simultaneous changes in the pressure of the ventricle and aorta just described can also be demonstrated by means of the differential manometer of Hürthle[1] (Fig. 140). It may be stated as the result of experiments made with different kinds of manometers that the average pressure of the right ventricle is about one-third that of the

FIG. 140.

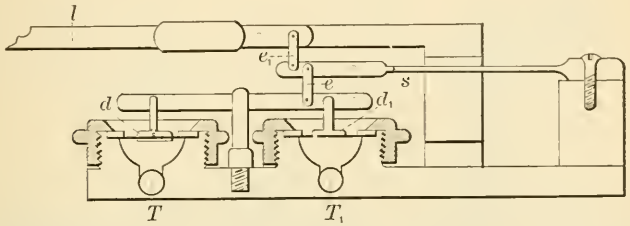


Diagram of the differential manometer of Hürthle. (FOSTER.) T, T_1. The tambours of two membrane manometers, the mouths of the tubes opening into each being shown in section. d, d_1. Central disks of tambours, working on a balance above them, the latter remaining horizontal as long as the pressure in the tambours is equal, but moving upward or downward with any difference in pressure, and, in working against the spring s by means of e and e_1, moves the lever l.

left, and as the pressure of the right auricle is only one-tenth that of the right ventricle, it would be only one-thirtieth that of the left ventricle.

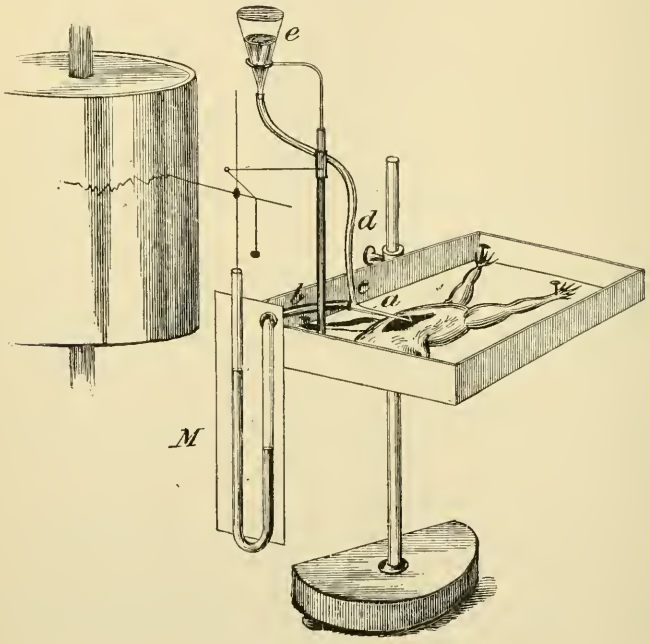
While the flow of the blood through the arterial system generally is influenced by the length of the vessel, friction, etc., the capillary system, as we shall see, is the constant source of resistance. In proportion to the fulness of the capillaries a greater or less obstacle is offered to the flow of the arterial blood. The force that the heart exerts must then vary according to the resistance to be overcome.

Arterial pressure is due, therefore, not only to the force exerted by the heart from behind, *vis a tergo*, but to the resistance offered by the capillaries in front, *vis a fronte*. This is readily shown by means of the Coats[2] or Marey[3] apparatus, but, as both these methods involve taking the heart out of the animal, and as it is desirable to show the phenomena, the heart being in situ, the author usually makes use of Brubaker's frog manometer (Fig. 141). This consists of a mercurial manometer M like that we have used in determining the blood pressure in the rabbit, only that it is smaller. The arterial canula differs, however, from the one used

[1] Pflüger's Archiv, Band xlix., 1891, s. 29.
[2] Sanderson, Handbook Physiological Laboratory, p. 268. [3] Op. cit., p. 70.

in that experiment. In this instance the end a of a ⊥-shaped glass tube is inserted into the bulbus arteriosus of the frog, the end b being adjusted to the proximal end of the manometer, while the stem c is connected by the tube d with a funnel e containing a solution of sodium carbonate. The funnel corresponds to the pressure bottle in the experiment with the rabbit. The frog is secured to a piece of cork, which rests within the stand supporting the manometer; the stand can be raised or lowered upon the vertical rod; the latter also supports, by the horizontal rod, the funnel. Having first determined the normal blood pressure, it will then be

Fig. 141.



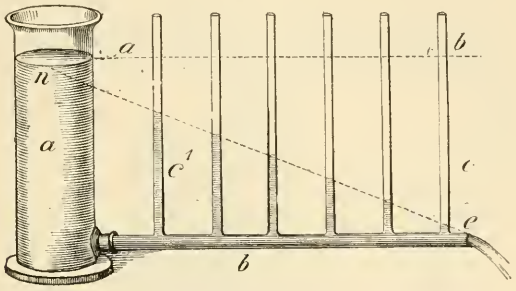
Brubaker's frog manometer.

observed that as the tube d is compressed, an obstacle being thereby interposed to the flow of blood from the aorta, the pressure will be increased, the mercury rising in the distal limb of the manometer, thus showing that the force which the heart exerts is proportional to the resistance to be overcome.

It is hardly necessary to state that the constriction of the tube in the last experiment would represent a capillary obstruction in the living animal. Theory and experiment, therefore, agree in showing that the amount of force which the heart usually exerts is far less than the possible force that can be put forth if occasion demands it. Assuming that the blood flows through the arteries, according to hydraulic laws, we should expect to find the pressure

diminishing as we recede from the heart to the periphery. Thus, if we watch the colored fluid as it flows from the reservoir (*a*, Fig. 142) through the horizontal tube *b*, it will be observed that the height to which the fluid rises in the vertical tubes c^1 and *c*, inserted into the horizontal one gradually diminishes as we recede from the first (c^1) to the sixth tube (*c*). In the present experiment,

Fig. 142.



Decrease of pressure in tubes of equal caliber.

where the colored fluid rose in the first tube to a height of 27 cm. (10.8 inches) in the sixth to a height of only 9 cm. (3.6 inches), the level of the fluid in the remaining tubes (2, 3, 4, 5) being intermediate between these extremes. This difference in the level of the fluid in the vertical tubes is caused by the resistance due to friction which the fluid encounters as it flows from the reservoir through the horizontal tube, and as the resistance encountered at the first tube gradually diminishes as we approach the sixth the height of the fluid or the pressure is proportionally diminished in the tubes as we pass from the reservoir to the outlet. Poisseuille[1] failed with his mercurial manometer to detect any difference in the blood pressure of arteries situated at different distances from the heart, such as theory indicated should have been found. Indeed, the difference in the blood pressure of two arteries, seen even when one is situated at a considerable distance from the heart, is too slight to be appreciable by the mercurial manometer alone. Volkmann,[2] however, showed by means of the kymograph, that there was a difference of 7 mm. (0.28 inch) mercury between the blood pressure in the carotid and metatarsal arteries of the dog, the pressure amounting in the first case to 172 mm. (6.8 inches), and in the latter to 165 mm. (6.6 inches). In the rabbit the difference between the blood pressure in the carotid and femoral arteries is only about 5 mm. ($\frac{1}{5}$ of an inch); in the calf, however, the difference amounts to 26 mm. (1.04 inches).

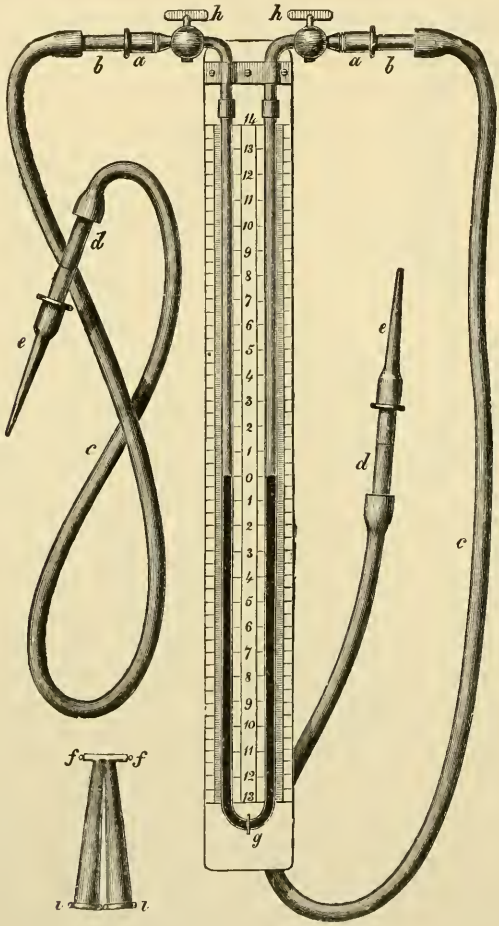
It is not only desirable to determine whether there exists any difference in the blood pressure of two arteries like the carotid and metatarsal, but also if the pressure in two arteries like the two

[1] Op. cit., p. 37.

[2] Op. cit., s. 167.

carotids or the two crurals is equal or different. With this object as well as of determining the difference between the pressure in an artery and a vein, the carotid and the jugular vein, for example, we make use of the differential manometer of Bernard [1] (Fig. 143). This consists of a U-shaped glass tube firmly supported upon a stand which carries a graduated scale, and by means of which the

Fig. 143.



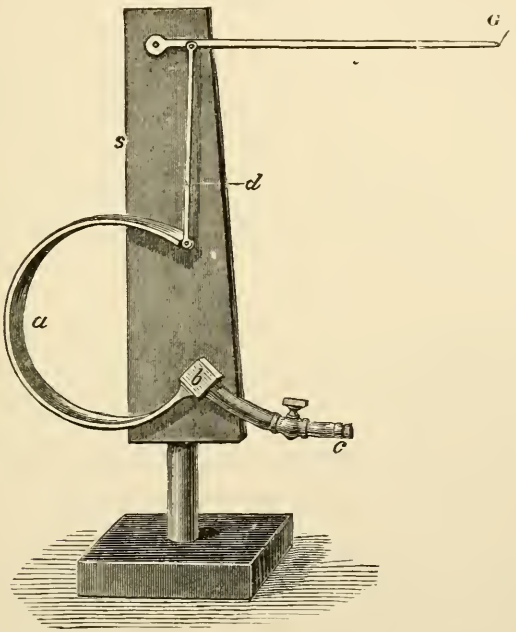
Differential manometer of Bernard.

tube is filled with mercury to a certain level. The two ends of the U-tube are adapted to lead pipes which are connected with the pressure bottle containing the solution of soda, and at *e e* with arterial canulæ to be inserted into the vessels to be examined. By means of the stopcocks either one or both the vessels can be placed in

[1] Systeme Nerveux, Tome i., p. 281.

communication with the manometer. Suppose, for example, the two ends of the manometer have been inserted by means of the arterial canulæ into the carotids of a rabbit. Having opened both stopcocks and removed the clamps from the arteries and allowed the blood to press against the solution of soda, it will be observed that the level of the mercury remains unchanged, showing, therefore, that the blood pressure in the two arteries is the same. If now one of the stopcocks be closed, at once the mercury will rise in the limb of the tube of the corresponding side, and by doubling the height to which the mercury is elevated, and deducting 1 mm. for

FIG. 144.



Fick's spring kymograph. *a*. C-spring. *s*. Support. *d*. Rod which communicates the movements of the spring to the lever *l*, and thus to the writing-needle *G*. *c*. Leaden tube by which the cavity of the spring is in communication with the artery.

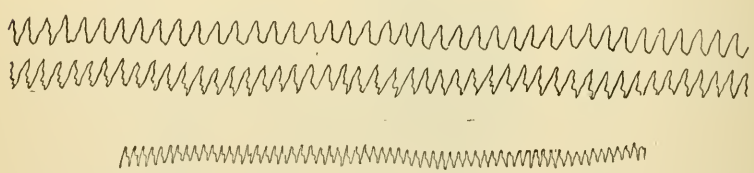
every 10 mm. of solution of sodium carbonate used, the blood pressure of the artery on the side where the stopcock remained opened is obtained.

Admirable an instrument as the kymograph undoubtedly is, and however accurately it fulfils its purpose, it must not be forgotten that the trace recorded on the cylinder is due to the oscillations of the mercury, and, therefore, only indirectly to the pressure of the blood. On account, however, of the inertia of the mercury and the suddenness of the expansion of the artery, the oscillations of the mercury, though caused by the pressure of the blood, are not an exact measure of it, since by the time the mercury has risen to its

highest elevation the artery has collapsed. If the heart is beating very quickly the extent of the oscillations of the mercury is relatively too small, and if the interval between the pulsations is prolonged the excursion of the manometer is too great. The use of the mercurial kymograph is, therefore, limited to the study of the mean pressure and of variations in pressure, such as occur at sufficiently long intervals to prevent the oscillations being mixed up with those proper to the instrument. In order to study the variations of blood pressure in the exact order in which they occur, and as regards their duration and degree, etc., we make use of Fick's spring kymograph, which is so constructed that it transmits the movements communicated to it without obscuring them by any movement of its own.

The instrument (Fig. 144) consists essentially of a hollow C-shaped thin metal spring (*a*) filled with alcohol and communicating through its proximal end (*b*) by means of a connecting tube (*c*) with the pressure bottle containing the solution of the sodium bicarbonate and the arterial canula. The proximal end of the spring being fixed, as the blood pressure increases the spring tends to straighten itself and the distal or free end makes the movements which follow exactly the variations in the arterial tension.[1] These

FIG. 145.



Traces in rabbit taken with Fick's spring kymograph.

movements are most exact, the slightest variations in the blood pressure being expressed by them. As they are, however, very small before being recorded, they are enlarged by the lever which is carried by the distal end of the spring. It will be seen from Fig. 145, illustrating a trace of the blood pressure in the carotid artery of the rabbit, taken by the spring kymograph, that the ascent of the lever, due to the expansion of the artery caused by the ventricular systole, is very abrupt, almost vertical, that at the vertex the direction of the trace is horizontal, that the lever in its descent pursues an oblique course at its termination, being also horizontal in direction, and that the dicrotism of the pulse is very evident. The nature of these peculiarities we have already considered in describing the pulse. If we wish to express in millimeters of mercury the absolute blood pressure determined by the spring kymograph, the instrument must first be graduated by comparison

[1] In some recent forms of Fick's kymograph the membrane of a small air drum works against a horizontal slip of steel which acts as a spring.

with a mercurial manometer. This is done in the following way: The spring kymograph being so placed that it will write on the recording cylinder, its connecting tube in communication with the pressure bottle is adapted to the proximal end of the mercurial manometer. The pressure bottle is first lowered until the solution it contains stands at the same level as that of the mercury in the manometer. The clockwork being put in motion the cylinder revolves and a trace is taken which will represent the abscissa. The pressure bottle is then raised till the mercury is elevated in the distal limb of the manometer 10 mm. ($\frac{2}{5}$ of an inch) higher than in the proximal one, and a second tracing taken, and so on until we have attained a number of tracings parallel with the first one or abscissa, and therefore with each other. The vertical distance between the abscissa, and these lines or the ordinates measured in millimeters expresses then the value of the tracing in millimeters of mercurial pressure.

We have already alluded incidentally to the influence of respiration in modifying the curve of the blood pressure, and, as we have now seen, how the latter may vary according to the part of the vascular system generally. It is probable, also, that the blood pressure depends, to a certain extent, upon the size of the animal, the period of life, and general health, *cæteris paribus*, the blood pressure being greater in larger than in smaller animals, in those of middle age than in very young or very old animals, in strong, healthy than in weak, sickly ones. Inasmuch as the pressure of the blood depends upon the muscular force of the heart, and as the muscular substance of the heart, like all other muscle, is nourished by the blood, it follows that loss of blood in weakening the heart fibers should diminish blood pressure. The experiments of Hales[1] and Colin[2] have shown that such is the case, the blood pressure being diminished in proportion to the amount of blood lost. Finally, we shall see that the vasomotor nerves, in modifying the calibre of the vessels, greatly influence the blood vessels. In concluding our account of the arteries, there still remains for consideration the velocity with which the blood flows through them.

Physiologists at one time endeavored to determine the velocity of the blood by means of the theorem of Torricelli, assuming that the velocity with which a fluid escapes from a reservoir may be learned from observing the height to which it will flow into a vertical tube connected with the same, the velocity being equal to that which a body would acquire falling *in vacuo* through a distance equal to the height which the fluid attains in the tube, which is nearly the same as the level of the fluid in the reservoir. Little or no importance, however, can be attached to this manner of determining the velocity of the blood in the arteries, since the cardiac energy is expended in not only imparting a velocity to the blood but in overcoming re-

[1] Statical Essays, Vol. ii., p. 16. London, 1740.
[2] Milne Edwards, Physiologie, Tome iv., p. 115.

sistance, and unless the latter factor is known and be taken into account the velocity obtained by theory will be a gross exaggeration. Assuming, according to well-known hydraulic principles that the velocity with which a fluid, in a given time, flows through a tube is equal to the ratio of the efflux to the sectional area of the tube, Hales[1] estimated that the blood in the horse flows from the left ventricle into the aorta at the rate of nearly 17 inches in a second, which we will see agrees closely with the velocity recently determined by experiment.

Passing by the early attempts to determine the velocity of the blood such as those just mentioned, and which have now only a historical interest, let us endeavor to determine, not what the velocity of the blood ought to be in an artery according to theory, but what the velocity actually is in a living animal by experiment. The hæmodromometer (Figs. 146, 147), the instrument invented by

FIG. 146.

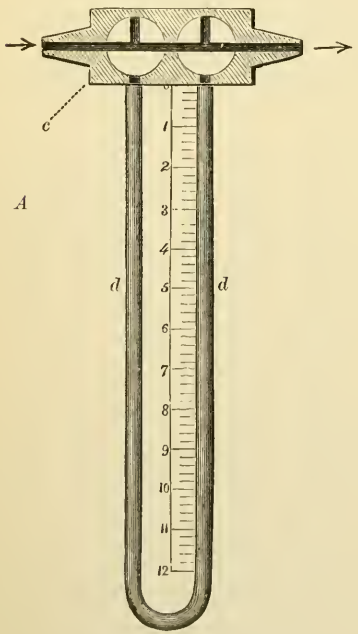
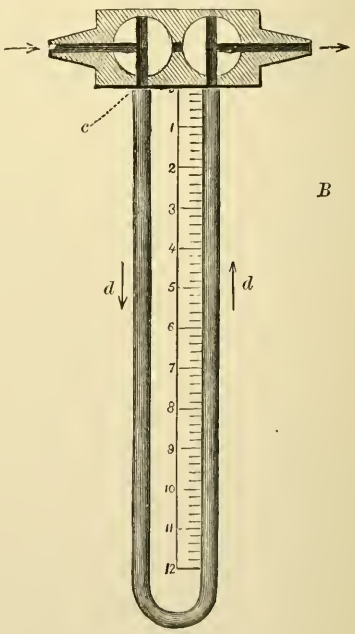


FIG. 147.



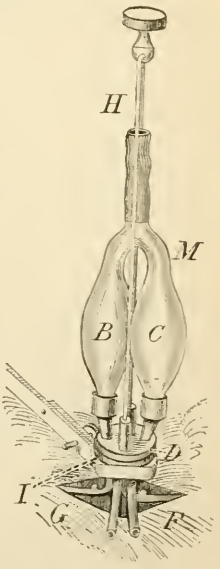
Volkmann's hæmodromometer for measuring the rapidity of the arterial circulation.

Volkmann[2] for this purpose, consists of a metallic tube (*c*), which is united to the two ends of a divided artery, and through which the blood can flow in the same direction as through the vessel itself (Fig. 146). To the metallic tube is attached laterally a U-shaped glass tube (*d*), containing water. By turning stopcocks the metal tube is put in communication with the U-shaped tube in such a way

[1] Statical Essays, Vol. ii., p. 46. [2] Hæmodynamik, s. 185.

(Fig. 147) that the blood cannot pass at once as it did before from the artery through the metal tube to the artery again, but must first pass through the U-shaped tube. The length of this tube being known, and the time it takes for the blood to flow through it being observed, the velocity with which the blood flows through the artery can be determined approximately. There are objections, however, to the use of this instrument, as the blood does not flow through the glass tube as easily as it does through the artery, both on account of the curvature of the tube and of the difference in its substance as compared with that of the artery, and as the blood flows from the proximal end of the artery into the glass tube it drives ahead the water it contains into the distal end, the effect of which is to contract the vessels, and so further retard the flow. It is for these reasons, that Volkmann's estimate of the velocity of the blood, for example, in the carotid artery of the horse of 254 millimeters (10.2 inches) in a second is too low.

Fig. 148.



Ludwig's stromuhr.

By the invention of the stromuhr, in 1857, Ludwig[1] greatly improved Volkmann's method of measuring the velocity of the blood. This instrument, also called the rheometer (*ῥεω*, to flow, *μετρον*, a measure), consists (Fig. 148) of two glass bulbs (*B*, *C*) of an ovoid shape, and of a known capacity, communicating superiorly by the curved tube and terminating so inferiorly as to be screwed into the canulæ *F* and *G*, which are only large enough to be inserted into the cut ends of the artery to be examined. The canulæ having been ligated, and the vessel previously clamped, by means of the small tube opening into the communicating tube, the bulb *C* is filled with olive oil up to the mark *M*, the bulb *B* with serum. The small tube is then closed. The clamps having been removed, the blood flows from the proximal end of the artery by means of the canula *F* into the bulb *C*, driving the oil ahead of it through the communicating tube into the bulb *B*, the serum in the latter being driven out of it through the canula *G* into the distal end of the artery. So far the method of experimenting with the stromuhr is essentially the same as that of the hæmodromometer, with these two differences, however, that serum being used instead of water there is less resistance offered to the flow of the blood, and, on account of the shape of the bulbs, a greater quantity of blood can be used, which is also of advantage. The great improvement, however, in Ludwig's instrument, as compared with Volkmann's, consists in this, that by turning the vertical rod *H*

[1] Dogiel, Berichte über Die Verhand. Der Kon Sachsischen Gesell. Der Wissen. Zu Leipzig, 1867, s. 200.

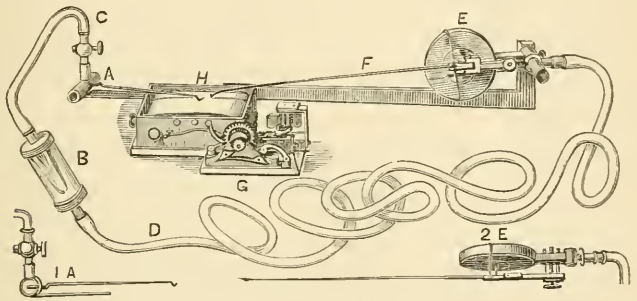
through 180 degrees, by a simple mechanical arrangement, the bulb *B* now filled with oil communicates through the canula *F* with the proximal end of the artery, and the bulb *C* filled with blood communicates through the canula *G* with the distal end. The blood still flowing from the proximal end of the artery will now drive the oil out of *B* into *C*, and the blood displaced by the oil will pass into the distal end. By turning the rod back again the bulb *C* will communicate with the canula *F*, and the bulb *B* with the canula *G*. This operation can be repeated several times before the blood coagulates.

To illustrate the manner in which the velocity of the blood is determined in a living animal by the stromuhr we will suppose that the instrument has been adapted to the carotid artery of a rabbit. The animal having been firmly secured and the artery exposed and clamped in two places, the clamps being separated by a distance of two inches, about an inch of the intervening vessel is cut out. The stromuhr being attached to the vertical stem of the holder by the horizontal rod and the bulbs having been previously warmed and their ends screwed into the canulæ which have been inserted into the cut ends of the artery, the bulb *C* is then filled with oil up to the mark *M*, it containing then 5 c. cm., and the bulb *B* with serum. The clamps are now withdrawn from the artery and the blood from its proximal end will be observed to drive the oil from *C* into *B*, the oil displacing the serum in *B*, which passes into the distal end of the artery. The moment that the blood reaches the level of the mark *M* the movable disk *D* is rotated as rapidly as possible through 180 degrees with the effect of putting the bulb *B* filled with oil in communication with the proximal end of the artery and the bulb *C* filled with blood in communication with the distal end of the vessel. The blood continuing to flow, the oil is now driven from *B* into *C*, the disk being rotated back again the moment that the blood reaches the level of the mark, the bulb *C*, now filled with oil, communicates as at first with the proximal end of the artery. The experiment may be continued in this way for a minute or more until the blood begins to coagulate. Inasmuch as we learn how often in a given time a definite quantity of oil is displaced by the blood we learn how much blood is delivered by the carotid artery in that time. Suppose, for example, that in an experiment 5 c. cm. of blood have been delivered by the carotid artery 10 times in 100 seconds—that is, 50 c. cm., then 1 c. cm. of blood has flown from the artery in 2 seconds, or 0.5 c. cm., equal to 500 mm. in 1 second. Dividing this amount by the sectional area of the artery through which it has flown—that is, by 3.14 mm. ($1^2 \times 3.14 = 3.14$), the diameter of the artery and the canula being nearly the same, 2 mm., and the radius, therefore, 1 mm., we get the velocity, nearly 158 mm. (6.3 in.), in 1 second $\left(\frac{500}{3.14} = 158.9\right)$, the hydraulic principle involved being that the

velocity equals the ratio of the quantity of fluid delivered to the sectional area of the tube.

The stromuhr is a most excellent and reliable instrument, as it interferes so little with the circulation, the flow of the blood being only stopped during the instant that the disk is rotated and the blood pressure being little altered by its passage through the instrument. This can be shown by connecting a manometer with the two tubes which are in communication with the bulbs, but which are not seen in the illustration, the tubes being placed in the side of the apparatus not shown in the figure.

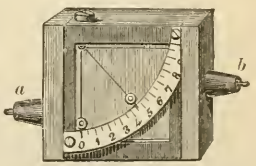
Fig. 149.



Hæmodromometer of Chauveau and Lortet.

While the stromuhr is admirably adapted to determine the exact amount of blood passing through an artery and the mean velocity of the flow, it does not, however, enable us to determine the incessant variations experienced by the blood as regards its velocity. For this object physiologists make use of the hæmodromometer of Chauveau. The construction of this instrument, like the hæmatachometer of Vierordt,[1] is based upon the principle of measuring the velocity of the blood by observing the amount of deviation undergone by a pendulum, the free end of which is suspended in the blood current, the amount of deviation being proportional to the velocity. It is essentially the same kind of instrument as the hydrostatic pendulum used by engineers to measure the velocity of a current of water. Chauveau's hæmodromometer, invented in 1858,[2] consists of a brass tube (Fig. 149, A), which is inserted into the cut ends of a divided artery, or into the slit made in the vessel of the horse and ligated. Part of the wall of the tube is of India-rubber membrane fastened over a longitudinal opening in the tube, and through which passes a light lever. The short expanded arm of the lever hangs freely in the

Fig. 150.



Hæmatachometer of Vierordt. *a*, *b*, for insertion into the cut ends of the artery.

[1] Die Erscheinungen und Gesetze der Stromgeschwindekeit des Bluts, 1858, s. 10.
[2] Journal de la Physiologie, Tome iii., p. 695. Paris, 1860.

blood, and is moved through a greater or less arc, according to the force with which the blood rushes against it, in from the artery, the India-rubber membrane acting as a fulcrum. The movements of the long arm of the lever *H* in the opposite direction to those of the short one are measured by means of a graduated scale. The long arm of the lever, it will be observed, projects considerably from the tube A. In order to determine the actual velocity of the flow in addition to the varying changes the instrument must be first experimentally graduated. This can be done in the following way: A current of warm water, or, better, defibrinated blood, is made to pass through the tube of the hæmodromometer with such a velocity that the deviation undergone by the pendulum is the same as when the instrument was inserted in the artery. The velocity of the current can be easily determined by receiving the fluid from the tube in a graduated vessel, and observing the time occupied in discharging a given quantity.

When a marker is attached to the end of the long lever *H*, the movements can then be recorded on the cylinder, and we obtain a graphic representation of the velocity and its variations. The hæmodromometer, when used in this way, becomes the hæmodromograph. Lortet[1] has modified Chauveau's instrument so that a trace of the blood pressure can be taken simultaneously with that of the velocity. This is accomplished (Fig. 149) by putting in communication with the tube A the lever of which through its movement gives a trace of the velocity of the blood, a sphygmoscope (B), the blood from the artery after passing through the tube A, enters the caoutchouc bladder B, of the sphygmoscope, and expanding, it compresses the air in the glass, which, acting through the tube D, upon the recording lever *F*, gives the trace of the blood pressure.

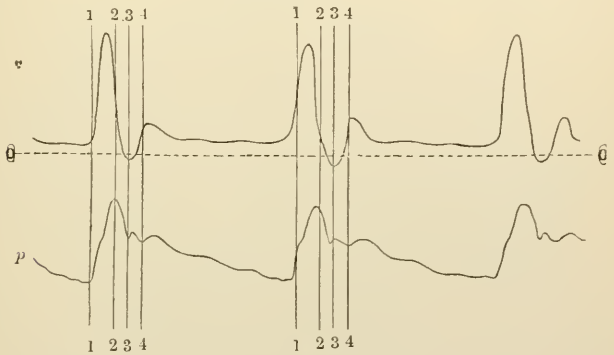
Chauveau has determined, by means of his hæmodromometer, that the velocity of the blood in the carotid of the horse at each ventricular systole is about 50 cm. (20 in.) in a second; this velocity, however, gradually diminishes until finally the blood, for a moment, stops moving altogether. Immediately following the systole and synchronous with the closure of the semilunar valves, a second impulse is given to the blood by the recoil of the arterial walls, and the blood moves now at a rate of about 20 cm. (8 in.) a second; this velocity gradually diminishes, the average rate being, until the next ventricular systole, about 12 cm. (4.8 in.) in a second. It will be observed, from these experiments, that the velocity of the blood is at times much more rapid than at others. This is, however, only true of the arteries near the heart, like the carotid, the acceleration of the velocity, like the pulse, gradually disappearing in the small arteries, and for the same cause, the gradual diminution of the cardiac pressure, as we recede from the heart to

[1] Recherches sur la vitesse du cours du sang dans les artères du Cheval an moyen d'un nouvel hémodromographe, Paris, 1867.

the periphery. While the velocity of the blood in the arteries in man can be experimentally determined from the experiments made upon the horse, approximately, it may be considered as not differing very much from that observed in that animal. The velocity of the blood in the arterial system is not only modified, as we have seen by the cardiac pressure, but is influenced by other causes.

It has already been mentioned that the capacity of the arterial system increases as we pass from the aorta to the capillaries, and as fluids move more slowly in the wide tubes than in narrow ones, the velocity of the blood ought to be slower in the peripheral arteries than in those near the heart. Experimentally, this has been shown to be the case; according to Volkmann, the velocity of the blood in the metatarsal artery in the dog is only 5 cm. (2 inches), that of the carotid artery being 25 cm. (10 inches) in the second. The velocity of the blood will vary, also, according to the resistance offered to its flow; the compression of an artery, for example, offering an obstacle to the circulation, will diminish the velocity, and even stop the movement altogether. The amount of resistance offered by the capillaries greatly influences the velocity of the blood. The capillary resistance remaining constant, an increase in the force of the heart will increase the velocity; a diminution in the cardiac force will diminish it. On the other hand, the force of the heart remaining constant, the velocity of the blood will be either increased or diminished, according as the capillary resistance is increased or

FIG. 151.



Tracings of variations of rapidity and of pressure of blood in the carotid of a horse, obtained by Chauveau and Lortet. The line *v* represents the curve of the rapidity of the blood; and *p* the curve of arterial pressure. The figures and vertical lines represent corresponding periods in the tracings. (McKENDRICK.)

diminished. It will be observed from what has been said in reference to the pressure of the blood and its velocity, that, with the increase or diminution of the one we have often a corresponding increase or diminution of the other. Thus, when the action of the heart is diminished by stimulation of the pneumogastric nerve, the velocity and blood pressure are diminished at the same time. The

relation of the two, however, may be an inverse one—that is, the velocity may be diminished, and yet the blood pressure may be increased; for example, if an artery be compressed the velocity is diminished, and yet the blood pressure rises, as we have seen. Any influence which increases or diminishes the force of the heart, which propels the blood toward the periphery, will increase or diminish at the same time the velocity and blood pressure, as in the example just given of the effect of stimulation of the pneumogastric nerve; on the contrary, any influence which will increase or diminish the resistance to the arterial flow will make the velocity and blood pressure vary in the inverse relation toward each other. Thus, if the capillary resistance be very great the velocity is diminished but the blood pressure rises.

On account of this relation between the pressure of the blood and its velocity, wherever it is practicable the two should be studied together (Fig. 151), since it is impossible to learn from the elevation of the mercury in the manometer alone whether the rise in the blood pressure is due to increased cardiac action, or increased peripheral resistance. If, however, the trace of the velocity be taken simultaneously with that of the blood pressure, and it is seen that the velocity is diminished, then the rise in the blood pressure will be due to peripheral resistance; on the other hand, if the velocity be increased, then it is due to increased heart action. The want of such comparative observation leaves us often in doubt as to what the rise in the blood pressure, as indicated by the elevation of the mercury, was really due to in many of the recorded experiments upon blood pressure. The result of Chauveau's observation upon the coronary arteries with his hæmodromograph illustrates the importance of this comparative method of experimentation. It being demonstrated that, during the systole of the ventricle, the velocity of the blood is diminished in the coronary arteries, the rise in the blood pressure observed must be due to peripheral resistance, the contracted state of the muscular substance of the heart during the systole offering an obstacle to the flow of the blood through the coronary arteries; the velocity being increased, however, during the diastole, and the blood pressure falling, shows that the obstacle has been removed, the muscular fibers of the heart now being relaxed. The above view is a confirmation of what has been already said in reference to the circulation of the blood through the substance of the heart itself.

CHAPTER XVIII.

CIRCULATION OF THE BLOOD.—(*Continued.*)

THE CAPILLARIES.

The capillaries (Fig. 152) discovered by Malpighi,[1] in 1661, are the minute vessels through which the blood (with few exceptions) flows from the arteries to the veins. As an artery becomes smaller and smaller it gradually loses its external and middle coat, and, to a great extent, its internal one also, the endothelial layer alone remaining. This constitutes a capillary. As the capillary approaches the vein it not only becomes larger, but changes the character of its structure, developing gradually three coats, until finally the capillary becomes a vein. Practically, it is impossible to say exactly where the artery ends and where the capillary begins, or where the capillary ends and the vein begins, the transition

Fig. 152.

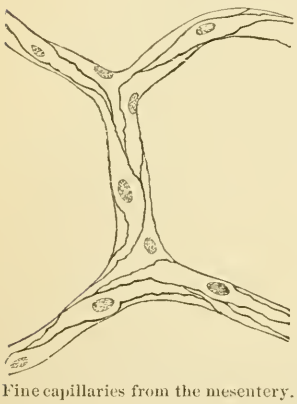
Capillary plexus in the portion of a web of a frog's foot, magnified 110 diameters. 1. Trunk of vein. 2, 2, 2. Its branches. 3, 3. Pigment cells. (Carpenter.)

from one to the other is so gradual. It is for this reason that a difference of opinion prevails among anatomists as to what constitutes a capillary, and therefore the description of these vessels

[1] Marcelli Malpighi, Opera Omnia Lug Bat, 1687, p. 328.

differs, according to the view taken of their structure. According to some histologists there are various kinds of capillaries, differing from each other in the amount of muscular and fibro-elastic tissue present. Such vessels we would regard as either small arteries or veins, considering a capillary to be a transparent, apparently homogeneous, elastic and possibly contractile vessel whose wall consists of a single layer of flattened endothelial lanceolate cells with oval nuclei, joined edge to edge by the so-called cement substance and continuous with the endothelial layer of the arteries on the one hand, and with that of the vein on the other. The wall of the capillary varying between the $\frac{1}{480}$ to $\frac{1}{1000}$ of a mm. ($\frac{1}{12000}$ and $\frac{1}{25000}$ of an inch) in thickness, is apparently almost homogeneous, it is only after appropriate treatment with silver nitrate and carmine that the outlines of the cells composing it, with their nuclei, become apparent (Fig. 153). The length of the capillary—that is, the distance between the end of the artery and the beginning of the vein—varies, on an average, between the $\frac{1}{2}$ and $\frac{1}{5}$ of a mm. ($\frac{1}{50}$ and $\frac{1}{125}$ of an inch), the average diameter varying between the $\frac{1}{80}$ and the $\frac{1}{160}$ of a mm. ($\frac{1}{2000}$ and $\frac{1}{4000}$ of an inch).

Fig. 153.



Fine capillaries from the mesentery.

If the thickness of the wall of the capillary be deducted from that of the diameter of the vessel it will be found that in many instances the calibre of the vessel is so small as to permit of the red blood corpuscles passing through it only in single file. Indeed, in some cases the diameter of the red blood corpuscle is larger than that of the lumen of the capillary, and in order to pass through the latter it must change its shape, lengthening and narrowing itself, regaining, however, its proper form through its elasticity on passing into a larger vessel.

The small size of the capillaries, both as regards their length and breadth, has an important significance in reference to the amount of blood flowing from them into the veins. Thus it is well known, from the researches of Poisseuille,[1] that the amount of fluid discharged by a tube the $\frac{1}{100}$ of a millimeter in diameter ($\frac{1}{2500}$ of an inch) will be sixteen times that discharged by a tube the $\frac{1}{200}$ of a mm. ($\frac{1}{5000}$ of an inch), the amounts discharged being proportional to the fourth powers of the diameters—that is, $1 : x :: \frac{1}{200} : \frac{1}{100}$, or x equals 2 and 2^4 equals 16. On the other hand, the amount discharged by tubes of the length of the capillaries will be inversely as their lengths—that is, of two capillaries of different lengths more fluid will be discharged from the short vessel than the long one. It will be seen, therefore, that any change in the length or breadth

[1] Mem. de l'Acad. des Sciences Savant Etrang, Tome ix., p. 513.

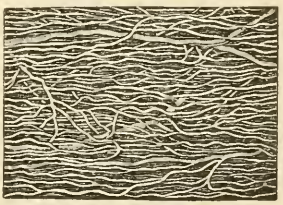
of a capillary will influence greatly the amount of blood delivered to the veins, and so increase or diminish the resistance offered by the capillary system to the arterial flow; the significance of which we have seen in considering the velocity of the blood and its pressure in the arteries. The cell-like structure of the capillaries just referred to makes perfectly clear how it is possible for the white corpuscles to pass from the capillary into the surrounding tissues. The capillaries, unlike the arteries and veins, constitute a true plexus of vessels of nearly uniform diameter, branching and inosculating in every direction. This inosculation is characteristic of the capillaries and the plexus is developed in proportion to the functional activity of the part. Thus the capillaries are very numerous and close set in the nervo-muscular and glandular tissues, absorbing surfaces, etc., structures in which the molecular changes incident to nutrition are peculiarly active.

While the general character of the capillaries throughout the system is the same, the difference in their disposition as regards their

Fig. 154.

Distribution of capillaries on the surface of the skin of the finger. (Carpenter.)

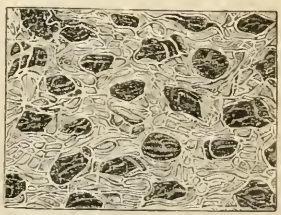
Fig. 155.



Distribution of capillaries in muscle. (Carpenter.)

closeness and the form of the network is often so marked that the histologist can frequently tell from what part of the body a tissue has been taken by an examination of the capillaries alone. No one can fail to recognize the difference in the arrangement of the capillaries in the skin (Fig. 154), as compared with that in muscle or mucous membrane (Figs. 155, 156). Capillaries, while found almost everywhere in the human body, are absent in certain structures like cartilage, hair, nails, etc., and hence such parts are often called extravascular. This name is apt, however, to mislead and is inappropriate, since all tissues are extravascular in so far as they lie outside of the vessel carrying the blood that nourishes them. In the vascular tissues the nutriment osmoses through the wall of the capillary into the tissue immediately surrounding the vessel and thence into parts more and more remote from it. In the so-called extravascular tissue the nu-

Fig. 156.



Distribution of capillaries around follicles of mucous membrane. (Carpenter.)

triment comes from the blood of a capillary, as in the vascular tissue, though the capillary may be situated at a considerable distance from the tissue that it nourishes. The only difference between the vascular and extravascular tissue is that the nutriment is conveyed a longer distance in the one case than the other; the difference, therefore, is one of degree, not of kind. There are no capillaries in the spleen, erectile tissues, and maternal part of the placenta, their place being supplied by blood sinuses. When we come, however, to the study of the development of these organs, we shall see that these blood sinuses are probably enormously dilated capillaries. It will be remembered that the arterial system was likened to a cone, of which the heart is the apex and the capillaries the base, and that the area of the branches of an artery is usually greater than that of the artery itself. We should expect, therefore, to find that the capacity of the capillary system is far greater than that of the arterial. Indeed, the microscopical examination of the skin, mucous membrane, muscle, etc., in which the capillary vessels have been injected gives the impression that such tissues consist of nothing but capillaries. This is also true almost to the same extent in living animals under certain conditions, thus during digestion the surface of the mucous membrane lining the alimentary canal presents a light red appearance through the distention of its capillaries with blood.

The capacity of the capillary system must be immense—indeed, according to Vierordt,[1] it is 800 times that of the arterial. This estimate, though only approximate, cannot be very far from the truth, being deduced from the law that the velocity with which a fluid flows through a tube is inversely as the diameter of the tube. We shall soon see, as an illustration of this law, that the blood flows much more slowly in the capillaries than in the aorta, the total area of the capillaries being far greater than that of the aorta. The sectional area of the capillary system being then to the sectional area of the aorta as the velocity of the blood in the aorta is to the velocity of the blood in the capillaries, the

$$\text{sec. area of capillaries} = \frac{\text{sec. area of aorta} \times \text{vel. of blood in aorta}}{\text{vel. of blood in capillaries}}.$$

$$840 = \frac{1 \times 14}{\frac{1}{60}}.$$

By dividing the total sectional area of the capillaries by the area of one capillary an approximate estimate of the number of capillaries can be obtained. It was in this way that Hales[2] calculated that there were over eight millions of capillaries in the human body. The general structure, distribution, etc., of the capillaries

[1] Die Erscheinungen und Gesetze der Stromgeschwindigkeiten des Blutes, s. 35.
[2] Statical Essays, Vol. ii., p. 69.

having been described, let us now consider the manner in which the blood flows through them.

As the phenomenon of the flow of the blood through the capillaries, as viewed by the microscope, is one of the most beautiful and striking spectacles in nature, a few words as to the most convenient method by which it can be observed appear necessary. For this purpose we generally make use of the mesentery of the frog, on account of it being so easily exposed and readily arranged on the apparatus supporting it, which is a very simple one, consisting of a thin piece of cork with an opening in it through which the light can pass, and upon which rests, slightly elevated, a glass slide, over which is placed the mesentery, the loop of intestine drawn out of the body to which the mesentery is attached resting in a little gutter or groove on the glass slide surrounding the opening. A few drops of a solution of sodium chloride (3 per cent.) being placed upon the mesentery and a slide cover placed over it, and the cork placed on the stage of the microscope, the circulation can be observed for a considerable time before inflammation sets up. The web of the frog's foot, its lung and tongue, may also be used for the demonstration of the circulation. The tongue of the frog, on account of its being attached to the anterior part of the lower jaw and free posteriorly, and therefore being easily drawn out of the mouth and through its great vascularity, is also a favorite subject of study with physiologists. When the tongue is used it is best, however, to inflate it first and then slit it open, when a magnificent view of the circulation is obtained. The tails of tadpoles, of little fish, and the gills of the salamander, are also serviceable objects for the study of the circulation. When the salamander is used it should be placed in a Holman's life slide, by means of which the animal is firmly secured without injuring it, while the water is constantly renewed. When the fish is used, Caton's fish trough will be found serviceable. This consists of an oblong box, one end of which transmits the light through an opening in the piece of glass upon which the tail of the fish in which the capillaries are to be examined is secured, the head and body of the fish resting at the other end of the box. By means of a cistern and tube, a constant current of water passes through the box.

The study of the capillary circulation in mammals is more difficult than in any of the animals just referred to, since, with the exception of the wing of the bat, there is no external part transparent enough to be observed with the high power of the microscope, and if any of the internal parts are used the effects of exposure are far more injurious than in the frog, for example. The mesentery and omentum of small rodents, like rats and mice, etc., have been often made use of in demonstrating the capillary circulation in the mammalia; but the omentum of the guinea-pig is preferable for many reasons, on account of its transparency and of its delicate and simple structure, consisting, to a great extent, of only two layers, of being

attached to only one side of the stomach, and little or no fat being present. The great difficulty experienced in observing the capillaries in the peritoneum of the mammalia is due to the injurious effects of exposing the membrane to the atmosphere and the risk of wounding it. To avoid this, the omentum, which is the part we use, is floated into a glass trough containing either serum or a solution of sodium chloride (3 per cent.), which is kept at the temperature of the body by means of the warm stage, which we have already described. The guinea-pig used should be put under the influence of chloral, three grains injected under the skin being sufficient for an animal weighing one pound, and then placed upon a support on a level with the stage of the microscope. The incision being made a little below the ensiform cartilage, and extending outward from the rectus muscle, about an inch from the edge, the omentum is carefully seized and drawn out into the trough. It is well to cover the parts of the membrane not immediately under the microscope with pieces of blotting-paper, in this way avoiding unnecessary exposure, and at the same time keeping the omentum steadier than it otherwise would be. With all the above precautions, however, the view of the capillary circulation thus obtained is far from satisfactory, and not comparable to that observed in the mesentery of the frog.

Since the time of Malpighi, the phenomena of the capillary circulation have been often described; but language is inadequate to give one any idea of the beauty of the spectacle, and to be appreciated it must be seen.

We will suppose the mesentery of the frog disposed within the field of the microscope as just described. Here may be seen the arterioles of the mesenteric artery through which the blood flows with apparently amazing rapidity, dividing and subdividing until the blood is carried to an exquisite network of delicate tubes resembling a web of fine spun glass, the capillaries, in which the blood is separated from the tissues by a thickness which has just been stated may vary between the $\frac{1}{480}$ and $\frac{1}{1000}$ of a mm. ($\frac{1}{12000}$ and $\frac{1}{25000}$ of an inch), but which in reality is so thin as to defy accurate measurement. It will be readily appreciated, therefore, with what rapidity the nutritive elements osmose into the tissues and the effete matters be taken up by the blood. Indeed, the capillaries are the seat of all physiological and pathological nutrition processes. The arteries and veins are only means toward an end, the one set of vessels carrying the blood to the part to be nourished, the other carrying it away laden with the waste products. It will be observed that the red blood corpuscles move in the middle of the stream, and if the capillary be large enough to admit of three corpuscles moving abreast, the middle one soon advances beyond the others, showing that the velocity of the current is greater in the middle than at the sides on account of the friction. Indeed, the blood moves so slowly where it is in actual contact with the

wall of the capillary that it appears immovable and has been called for this reason the "still layer." As might be expected, the friction so exerted is less in a wide than in a narrow tube, in a sluggish than in a swift stream. A red corpuscle is sometimes caught in the still layer, where it moves slowly for a time, turning over and over; sooner or later, however, it passes again into the central stream and in an instant is whirled out of sight. The white corpuscles, on the contrary, stick either to the still layer or to the capillary wall, and being quite numerous in the frog, a number are often seen at one time in the same capillary.

The difference in the behavior of the red and white corpuscles in this respect appears to be due solely to the red corpuscles being heavier than the white ones, or the leucocytes, it having been shown[1] that if a fluid holding in suspension two kinds of particles be driven through capillary tubes the lighter particles will go to the wall, the heavier ones to the middle of the stream. The corpuscles often move in such a manner that they appear as if they were endowed with consciousness and volition. Thus when the single rows of corpuscles flowing in two capillaries reach a third vessel, formed through the union of the other two, and only large enough to admit one row, one row will hold back until the other one has passed into the capillary and then will follow in its turn. Frequently the corpuscles will flow in one direction and meeting some obstacle will entirely reverse their course. A corpuscle is often retarded for some time by the angle formed by the division of a capillary into two, and may be observed turning over and over and changing its shape according to the pressure of the current until it is swept finally into the main stream.

Certain capillaries will be for a time quite empty, while others near by are filled with corpuscles, then one or two corpuscles will float into the empty capillary, in a moment or so a few more, and soon a current is established, while in the same gradual way a distended capillary may become empty.

Poisseuille[2] first showed that the law regulating the flow of liquids in tubes was applicable to such having as small a diameter as those of the capillaries, and it is an interesting illustration of the uniformity of the laws of nature that the same phenomenon of the rapidity of the flow of a stream being greater in the middle than at the sides is seen on a magnificent scale in the motion of a glacier, it being a matter of daily observation to those passing any time on a glacier to notice that the stones, débris, etc., move more rapidly in the middle of the glacier than those at the sides.

One of the most striking facts in the phenomena of the capillary circulation is the uniformity with which the blood flows through these vessels. The motion is here perfectly continuous; we no longer observe either the intermittent or remittent action so charac-

[1] A. Schklarewsky, Pflüger's Archiv, Band i., 1868, s. 603.
[2] Mem. de L'Acad. des Sciences, Sav. Etrang, T. vii., 1835, p. 45.

teristic of the heart and arteries. We observe that the flow of the blood in the capillaries is never the same for any length of time—indeed, one of its most interesting peculiarities is the constant manner in which the scene varies—influenced as it is by so many conditions. In endeavoring to follow the course of the corpuscles as they flow through the capillaries, one's first impressions, seeing them often swept along as if in a torrent, is that the velocity of the flow must be very great. Reflection at once suggests to us, however, that in proportion to the power of the microscope used the velocity is magnified. The simplest way of determining the velocity of the blood in the capillaries is to substitute for the ordinary eye-piece of the microscope an ocular micrometer, and with a reliable watch held close to the ear to determine the time that it takes a blood corpuscle to pass across the field of the microscope, or the interval of space included between two or more divisions of the micrometer. Weber[1] was the first, we believe, to make use of this method. It was in this way that he determined the velocity of the blood in the capillaries of the tail of the tadpole to be about the $\frac{1}{2}$ of a millimeter in a second (the $\frac{1}{50}$ of an inch). Valentin[2] estimated the velocity in the capillaries of the web of the frog's foot was about the same—in round numbers, about 2.5 cm. (one inch) in a minute. According to Volkmann,[3] the velocity of the blood in the capillaries of the gills of the tadpole is $\frac{1}{5}$ of a mm., in the tail of a little fish $\frac{1}{10}$ of a mm., and in the capillaries of the mesentery of a dog, $\frac{8}{10}$ of a millimeter in a second—in round numbers, about 5 cm. (2 inches) in a minute.

Vierordt[4] makes use of an apparatus for measuring the velocity of the blood in the capillaries, which is based upon the fact that a body moving at a certain rate and illuminated but for a very short instant appears immovable. By placing between the mirror of the microscope and the object-glass a movable disk pierced with holes through which the light is transmitted, the object viewed is only seen when one of the holes passes across the axis of vision. If the length of time the blood corpuscle is illuminated be known and the blood corpuscle appear immovable, then the rate at which it is moving can be inferred. This physiologist has also calculated the velocity of the blood in the capillaries of the human retina. As is well known, the eye after a time becomes fatigued when exposed to a strong white light; if the eye be now compressed, one sees the image of a current in the form of a network. This appears to be due to the passage of the blood corpuscles through the capillaries of the retina. By calculating the space passed over in a given time by the image, Vierordt[5] estimates the velocity in this situation to vary between the $\frac{6}{10}$ and $\frac{9}{10}$ of a millimeter in a second. Assuming that the rapidity of the motion of the white corpuscles can be accepted as a means of estimating the velocity of the still layer, it

[1] Müller's Archiv, 1838, s. 467. [2] Physiologie, Band i., s. 482.
[3] Die Hæmodynamik, s. 184. [4] Op. cit., s. 35. [5] Op. cit., s. 112.

can be stated that on an average the current in the middle of the stream moves 9 to 17 times more rapidly than that at the sides. Inasmuch as the amount of blood required by the tissues varies very much from time to time, we should expect to find also great variations in the state of the capillaries in this respect. Thus at one time the capillaries supplying a tissue may be entirely empty or almost so, at another gorged with blood. It becomes important, therefore, to study the effects of such agents as will modify the caliber of these vessels or accelerate or retard the flow of the blood through them.

Among the most important of these may be mentioned the effects of cold, heat, electricity, certain local irritants, and changes in the physical and chemical composition of the blood. Thus a low temperature diminishes the quantity of blood in the capillaries and retards the circulation, while a high temperature, on the contrary, increases the amount and accelerates its velocity. The effect of cold upon the capillary circulation can be readily demonstrated by placing a piece of ice upon the part examined, the web of a frog's foot, for example, or the mesentery. The circulation will at once be observed to become much slower, stagnate, and often cease entirely, the capillaries are emptied and the small arterioles, those carrying usually two or three rows of blood corpuscles, will now admit only one row. If the ice be removed, the circulation will become normal again. If now the part examined be covered with water, say at a temperature of 40° C. (104° F.) or placed upon the warm stage at the same temperature, the quantity of blood in the capillaries will be greatly increased and the velocity so much accelerated, that it is with difficulty the corpuscles can be distinguished. The circulation can be at once arrested by the stimulus of electrical currents, the greatest effect being obtained when individual currents are used. The effect of the application of a local irritant, like a solution of common salt, when applied to the arterioles, and possibly also to the true capillaries, is at first to produce a constriction and a diminution in the velocity of the current. The constriction is, however, soon followed by a dilatation and the velocity is accelerated. This condition, however, lasts but a moment, an oscillation of the current begins, the velocity is diminished again, stagnation follows, the capillary becomes gorged with blood, the white corpuscles increase in number, and an inflammatory state is set up.[1]

It is well known that the composition of a fluid will influence the rapidity with which it flows through tubes of small diameter. Thus, solutions of potassium iodide and bromide, etc., flow more rapidly than solutions of sodium, calcium, and magnesium chloride, of sodium phosphate and carbonate. One would naturally infer then that the presence or absence of certain salts in the blood would

[1] Thompson: Lectures on Inflammation, Edinburgh, 1813, p. 51. Wilson Philip, Med. Chir. Trans., 1823, Vol. xii., p. 401. Wharton Jones, Guy's Hospital Reports, 1851, Vol. vii., 2d Ser., p. 24.

influence the rapidity with which it flows in the capillaries. Such was experimentally proven to be the case by Poisseuille,[1] the rapidity of the circulation in the horse being diminished by the introduction into the blood of ammonium acetate and sodium chloride. The influence of respiration upon the capillary circulation will be considered when the subject of asphyxia is taken up; while the effect of the vasomotor nerves in modifying the calibre of the arteries, and thereby affecting the quantity of the blood delivered to the capillaries, will be deferred until we study the nervous system.

In speaking of the effect of irritants when applied to the capillaries, it was just stated that a constriction of the arterioles, and probably also of the capillaries, was the first effect. It has long been, however, a subject of discussion as to whether the capillaries are really contractile in the same sense as the arteries. It is possible that the cause of the difference of opinion that still prevails in reference to this matter, may be due to the fact of one physiologist regarding as a capillary what another would consider an arteriole. The arterioles are, undoubtedly, contractile, their walls containing muscular fibers, and since the layer of nucleated cells of which the capillary wall consists is continuous with the contractile tunic of the arteriole, the capillary may possess true contractility. This seems to be the case, at least in the capillaries of the embryo, where the nuclei of the cells stand out through the contraction of the capillaries. On the other hand, the diminution in the calibre of the capillary, often supposed to be an evidence of its contractility, is really due to a diminution in the pressure of the blood, the wall of the capillary recoiling upon its contents through its elasticity, from a previous state of distention.

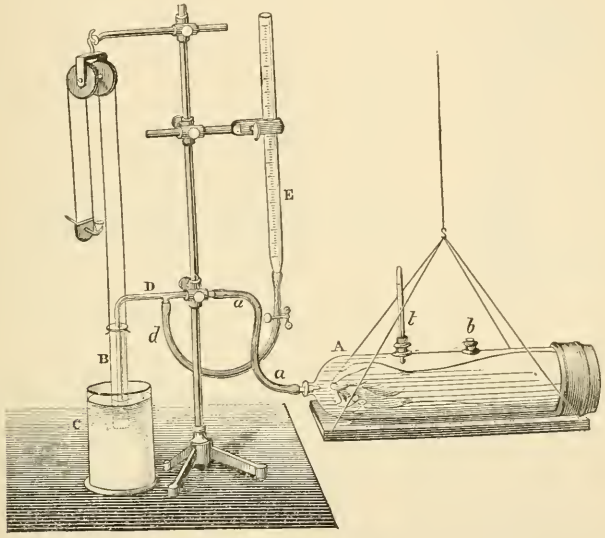
When a tissue which has been thoroughly injected, is seen under the microscope, it appears as if it consisted almost entirely of capillaries. It will be readily understood that any change, however slight, in the calibre of the capillaries will considerably influence the volume of the organ containing them. The changes in the volume of an organ will serve then as a measure of the amount of the contraction and relaxation of its capillaries. Physiology is indebted to Mosso more particularly for the employment of this method as a means of determining changes in the volume of the capillaries.

The plethysmograph (πληθος, bulk, γραφω, to write) devised by Mosso[2] for this purpose consists essentially of a large glass jar (A, Fig. 157), in which an arm is enclosed, for example, and communicating by a tube with a small glass jar (B), which is suspended in the water of the jar C by means of the pulley and weight. The jar A enclosing the arm is filled with water. With each increase in the volume of the arm the water is driven out of the jar A through the tube into the jar B, sinking it deeper in the water of

[1] Comptes Rendus de l'Acad. des Sciences, 1843, Tome xvi., p. 60.
[2] Atti Della Reale, Acad. delle scienze di Torino, xi., 1875, p. 21.

the jar C. With each diminution in the volume of the arm, the water is drawn back into the jar A, the jar rising out of the water in C. A pen adapted to the weight, records graphically upon a cylinder the elevation and depression of the jar B—that is, the changes in the volume of the arm examined. From the results of his experiments, Mosso concludes that the changes in the volume of an organ are due not only to variations in the blood pressure, but also to changes in the calibre of the vessels as well.

Fig. 157.

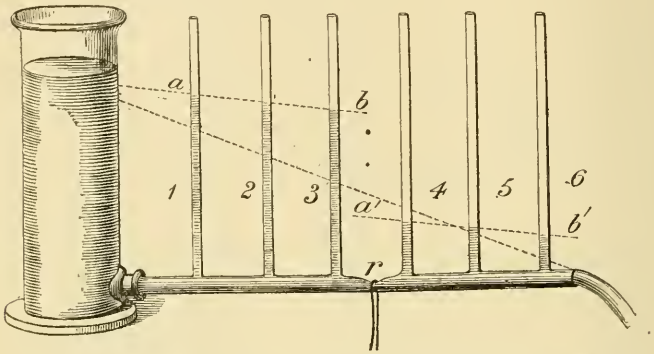


Plethysmograph of Mosso.

It will be remembered, that in speaking of the pressure of the blood in the arteries, it was shown that the pressure of a fluid gradually diminished as it receded from the source of the supply to the outlet, the diminution being shown by the different heights to which the fluid rose in the vertical tubes. Let us consider now what takes place when the fluid flows out of the apparatus (Fig. 158), which is almost the same as that just referred to, with the difference only that the diameter of the horizontal tube instead of being the same throughout its entire length, for a short distance in the middle (*r*), is very much diminished. We will consider this part as representing the capillaries, the horizontal portion of the tube on the left, the arteries, that on the right, the veins. It will be observed, as in the previous experiment, that the pressure diminishes very gradually and regularly in the tubes 1, 2, 3, corresponding to the arterial system, but that the pressure in the tubes 4, 5, 6, representing the veins, is very low, the blood passing from the arteries into the capillaries with difficulty, but readily passing out of the capillaries into the veins. Indeed, in the living animal at times, while the

arterial pressure amounts to 150 to 200 mm. of mercury, the venous pressure is almost nothing. Such a difference in the pressure implies that the capillary offers great obstacles to the flow of the arterial blood. If the experiment be modified by substituting a somewhat larger tube for the one representing the capillaries, the effect of this dilatation will be that the pressure in the artery, and

FIG. 158.



Apparatus to show decrease of pressure in tubes of unequal calibre. (MAREY.)

in the arterial end of the capillary, is diminished, while the pressure in the venous end of the capillary, and in the veins, is increased. Any influence, therefore, that favors the retention of the blood in the arteries, will diminish the quantity of blood in the veins, and *vice versâ*.[1] The dotted line (Fig. 158) represents the effect of substituting the large tube.

It is an everyday observation that when one compresses the skin with the finger, the part becomes pale, regaining its natural color, however, as soon as the compression ceases, the blood returning then to the capillaries. In order that the blood should be driven out of the vessels of the skin, the external force must be superior to the internal one, or the pressure of the blood. If we know the amount of compression used, then we can estimate approximately the internal force, or the pressure of the blood in the capillaries.

Upon this principle Kries[2] determined the pressure of the capillaries in a given area of the hand to amount when raised to 24 mm. mercury and lowered to 54 mm. mercury, the instrument (Fig. 159) made use of consisting of a glass plate to which was attached a scale pan on which weights were placed until the pressure exerted by the plate upon the skin made it pale.

While there can be no doubt that the heart is the main cause of the circulation, there are also good reasons for believing that there are other conditions than the contractile force of the heart and the

[1] Marey, op. cit., p. 357.

[2] N. V. Kries, Berichte über Die Verhandl. Der Kon. Sächsis. Gesells. Der Wissen. zu Leipzig, 1875, s. 149.

arteries which influence the flow of the blood through the capillaries. As is well known, in plants, and in many of the lower animals, the nutrient fluid is carried to all parts of the system in the absence of a heart; analogy would lead us to expect, therefore, that there must exist in the higher animals a similar force, a capillary power, so to speak, which may be masked by the influence of a centralized powerful heart. This so-called capillary force appears to be inseparably connected with the nutritive and secretory processes, since what increases or diminishes the one influences in the same way the other. The idea of such a force is not a new one, it is embodied in an ancient aphorism of *Ubi stimulus ibi fluxus*. That some such power exists in the capillaries of the higher animals, independent of the action of the heart, is shown by the fact that the blood will still continue to flow in the capillaries after the heart has ceased beating, while, on the other hand, the heart may still be acting, and yet the circulation will entirely cease in the capillaries of certain parts. Local variations in the volume of the blood flowing through the capillaries, the reversal of the current in the vessels, changes in their diameter, so often observed in the healthy living animal, cannot be attributed to the action of the heart, but are evidently due to an influence engendered in the walls of the capillaries themselves, or in the surrounding tissues.

FIG. 159.

V. Kries's apparatus for capillary pressure. A. Square of glass. (LANDOIS.)

Many pathological facts might be mentioned as illustrations of such local variations. Thus, in cases of spontaneous gangrene of the lower extremities, although the heart may be beating, and the arteries and the capillaries entirely pervious, nevertheless the blood will not flow through the capillaries, the stopping of the circulation being due to a difference in the capillaries themselves, and the surrounding tissues. Again, it has often been demonstrated, at least in cold-blooded animals, that the flow of blood through the capillaries will continue even after the heart has been completely excised. While this cannot be shown experimentally upon a hot-blooded animal, the shock experienced being so great from so severe an operation, nevertheless nature often does in a gradual way what we cannot show by experiment. Thus, as is well known, after the general death of the body, urine has flowed from the ureters, sweat exuded from the skin, and glands have secreted. Such phenomena can only be explained on the supposition that the blood has continued to flow through the capillaries after the heart has ceased to beat. It is well known, since the observations of Dr. Bennett Dowler[1] upon the bodies of individuals who have died of yellow

[1] Researches on the Capillary Circulation, New Orleans Med. and Surg. Journal, 1849.

fever, that the veins often become so distended with blood within a few minutes after death that when opened the blood will spurt from them a foot or more. The tonicity of the arteries can hardly be supposed to account for this venous jet, or for the empty condition in which the arteries are almost always found after death—but to some additional force in the capillaries themselves. Further, we shall see, when we come to study the development of the circulation in the embryo, that the blood begins to move first in the area vasculosa, that is toward the heart, not from it, and that the heart itself consists of cells so loosely attached together that it can be scarcely supposed to contract with force enough to account for the primitive circulation. Indeed, in the case of twins, it has been noticed that the heart in one of the two has even never been developed during the whole period of embryonic life, and yet the greater part of the organs were well formed. It might be supposed that the circulation in the twin in which the heart was absent was maintained by the heart of the one in which it was present, the blood from the one twin passing to the other through the vessels of the placentas, which were more or less in contact. This was shown by Dr. Houston[1] to be impossible, at least in the case reported by him.

In this connection the researches of Hyrtl[2] are interesting, that anatomist having shown that the placental vessels do not communicate in those cases where the twins are of the opposite sex. The facts of comparative anatomy, experiment, pathology, embryology, all harmonize in showing that there exists in the capillaries some force independent of the heart's action, which aids the flow of the blood through them. It has often been supposed that the contractility of the capillaries aids the flow of blood through them. Admitting that the capillaries are contractile, this force could only be exerted in a rhythmical manner by alternate contractions and dilatations, a kind of peristalsis; but no such movement is observed, the blood flowing through the capillaries as if they were glass tubes. Further, it can be experimentally demonstrated that a diminution in the diameter of the capillaries, whether it be due to true contractility, or simply to elasticity, retards the flow of the blood, the blood pressure rising. The capillary force cannot, therefore, be of such a kind.

On the other hand, the experiments of Weber[3] and Wharton Jones[4] have shown that electrical and chemical stimuli modify the capillary circulation, retarding the flow of the blood, and even producing complete stagnation, and yet no alterations in the diameter of the capillaries are observed, the change being evidently of a physico-chemical nature. Such facts, as well as those already referred to, show that there exists some mutual relation between the

[1] Dublin Medical Journal, 1837.
[2] Die Blutegefässe der Menschlichen Nachgeburt. Wien, 1870.
[3] Müller's Archiv, 1852, s. 361. [4] Op. cit.

blood, on the one hand, and the walls of the capillaries and the surrounding tissues, on the other.

It appears, then, that while the heart forces the blood into and through the capillaries, the rate at which it flows through these vessels will depend upon the general nutritive condition of the parts supplied by the capillaries, and that this capillary force can, under certain conditions, maintain the circulation independently of the heart.

Prof. Draper[1] suggests that the capillary force just referred to, may be of the same character as the force of capillary attraction, illustrating this view by the following experiment: "If two liquids communicating with one another in a capillary tube, or in a porous structure, have for that tube or structure different chemical affinities, movements will ensue, that liquid which has the most energetic affinity will move with the greatest velocity, and may even drive the other liquid before it." Thus, it will be noticed that if a capillary tube, containing gum, be immersed in a vessel filled with water, that the gum will rise in the tube, being displaced by the water, the water having a greater affinity for the walls of the tube than the gum. These experimental conditions are realized in the living body, the fresh arterial blood, on account of its oxygen and other nutritive elements, having a greater affinity for the tissues than the effete venous blood, hence the arterial blood will push forward the venous blood from the systemic capillaries toward the veins. On the other hand, in the pulmonary capillaries just the reverse obtains, the venous blood drives forward the arterial, since the former has a greater affinity for the inspired oxygen than the latter, in which the blood is already oxygenated. According to the same physical principle, the portal blood, containing the same elements out of which the bile is elaborated, having a greater attraction for the hepatic cells than the blood of the hepatic vein, the latter will be driven out of the hepatic capillaries into the hepatic veins. Indeed, there must be a continual movement going on in every part of the economy, each cell having a greater attraction for the blood containing its nourishment than for that blood which has nourished it. Such a movement undoubtedly supplements the force of the heart.

The consideration of the influence of the nervous system upon the capillary circulation, whether as modifying through the vasomotor nerves the calibre of the arteries, or acting directly by changing the nutrition of the parts, will be deferred for the present. In concluding our account of the circulation of the blood it remains for us now to describe the flow of the blood from the capillaries back to the heart through the veins.

[1] Human Physiology, 1878, p. 131.

CHAPTER XIX.

CIRCULATION OF THE BLOOD.—(*Continued.*)

THE VEINS.

In observing the flow of the blood through the capillaries, it will be seen that these vessels gradually pass into larger ones, the venous radicles, which in turn transmit the blood to the veins, the latter gradually uniting form two large trunks, the venæ cavæ, which, together with the coronary and cardiac veins transmit the blood to the right auricle of the heart while the pulmonary veins return it to the left.

The venous system may be regarded as consisting of two sets of veins, a superficial set returning the blood from the skin and surface generally, and a deep set which accompanies the arteries.

The veins differ in their structure from the arteries rather in degree than in kind, consisting essentially like the latter of three coats, an internal endothelial, a middle elastic muscular, and an external fibrous. The internal coat, consisting of subepithelial and elastic layers, is a continuation of the capillary, which we have seen is a prolongation of the internal coat of the artery. Indeed, it is practically impossible to say exactly where the artery ends and the capillary begins, or where the capillary ends and the vein begins, the transition from the one set of vessels to the other is so gradual.

The middle coat, containing the vasa vasorum, consists principally of fibrous tissue disposed in a longitudinal direction with some elastic fibers, and of a circular coat of elastic and muscular fibers mingled with some fibrous tissue. The external coat, like that of the artery, consists of white fibrous tissue, and in the largest veins, particularly in those of the abdominal cavity, there are a few unstriped muscular fibers arranged in a longitudinal direction. In the veins near the heart a few striated muscular fibers are present, derived principally from those of the auricle. These fibers are particularly well developed in the turtle. In certain situations in the cerebral sinuses, etc., the veins consist of little more than the internal coat with a few longitudinal fibers. Generally the veins adhere much more closely to the surrounding tissues than the arteries. Were such not the case, in many instances the vessels would collapse, the walls not being strong enough to resist external pressure. It may be also mentioned that it is through the intimate adhesion of the wall of the superior vena cava, jugular, subclavian, etc., to the surrounding aponeurotic layers that these vessels are kept open during inspiration.[1]

Many of the larger veins are provided with valves resembling

[1] Berard, Physiologie, Tome quatrième, p. 9.

those of the aorta and pulmonary artery (Fig. 160). They are usually found in pairs, and consist of crescentic semilunar doublings or folds of the internal coat or lining membrane of the vein strengthened with some included fibro-elastic tissue. These valves are usually situated opposite each other and project obliquely into the cavity of the vein or in the direction of the current. The convex portion of each valve is attached to the side of the vein, the concave edge is free and points toward the heart. Behind each valve the vein is dilated into a sort of pouch or sinus (Fig. 160) which prevents the valves adhering to the sides of the vein as the blood passes between them toward the heart. When, however, the blood passes backward toward the periphery, as we shall see it does under certain circumstances, it enters the sinus and getting behind the valves presses them toward each other and together and so prevents any further reflux.

Fig. 160.

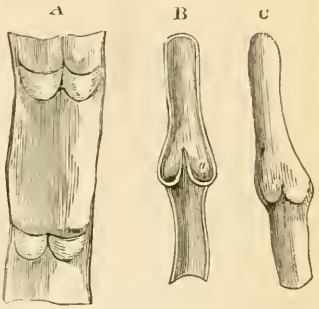


Diagram showing valves of veins. A. Part of a vein laid open and spread out, with two pairs of valves. B. Longitudinal section of a vein, showing the apposition of the edges of the valves in their closed state. C. Portion of a distended vein, exhibiting a swelling in the situation of a pair of valves. (Quain.)

The valves are so disposed, therefore, that while they offer no obstacle to the flow of the blood toward the heart, they effectually prevent to any extent motion in the reverse direction.

The valves are most abundant in the upper and lower extremities; the significance of this we shall see presently. The importance of the valves in the veins, though great physiologically, must not be exaggerated, since many veins have no valves. Thus in man at least, however it may be in other mammals, there are no valves in the venæ cavæ, in the innominate, pulmonary, portal, hepatic, renal, uterine, ovarian, spinal, and iliac veins. Further, there are very few valves in the veins of birds, reptiles, and fishes, and with the exception of that in the aorta, so-called, of the eolis, a small nudibranchiate mollusk, there are none in the veins of the invertebrata. It is evident, therefore, that the valves are not indispensable in the maintenance of the circulation.

The veins possess a considerable amount of elasticity. This is shown by the jet of blood which follows the puncture of a distended vein made in a portion of the vessel between two ligatures. The veins through their unstriped muscular fibers are also contractile, their caliber being slowly and gradually diminished through the application of electrical and other stimuli. The contractility of the veins can be more readily demonstrated in the frog and other batrachians than in mammals. The veins, like the arteries, are supplied and influenced by the vasomotor nerves, though not to the same extent. The veins, though much thinner and apparently

weaker, will usually resist a greater pressure than the arteries. Thus it was shown in the last century by Wintringham[1] that a greater force was required to rupture the vena cava and portal vein, for example, than the aorta. The method by which this was determined is as follows: An iron siphon containing a sufficient quantity of mercury, to which was screwed a glass gauge, and which communicated freely with a condensing syringe, was adapted to the artery or vein whose strength was to be tested. When the air in the sealed top of the gauge was compressed with a pressure equal to 158 pounds, the aorta in the ram, for example, burst, the vena cava of the same animal, however, resisting until the pressure amounted to 176 pounds. The strength of the portal vein was even greater than that of the vena cava. Wintringham, however, notices that the arteries of glands are stronger than the corresponding veins. Thus the splenic vein burst under a pressure of about 34 pounds, the artery supporting a pressure of 150 pounds. These experiments of Wintringham were very numerous and extended, being made upon the vessels of men, pigs, sheep, dogs, etc., and in the main have been confirmed by the later ones of Davy.[2] The significance of the greater strength of the veins, as compared with that of the arteries, usually observed, becomes at once apparent when we reflect upon the different amounts of pressure to which the two sets of vessels are subjected. We have seen that the pressure diminishes gradually in the arterial system, that the force of the heart is practically constant, and that the arterial pressure is being constantly relieved by the flow into the capillaries. On the other hand, the pressure into the veins varies according to the amount of blood delivered to them by the capillaries, regurgitation to any extent is impossible through the presence of the valves, while the heart offers a very restricted outlet. Thus portions of the venous system, from pressure in the veins, absorption of fluid, accumulation through gravity, etc., are subject to very great variations in pressure which the tenacity of their walls usually enables them to resist without injury. The ill effects of over-distention are, nevertheless, seen only too frequently in varicose veins, etc. The capacity of the venous system is much greater than that of the arterial—according to Haller,[3] in the ratio of 2.2 to 1. Usually a vein when distended contains more blood than the adjacent artery; the capacity of the pulmonary arteries, however, is about equal to that of the corresponding veins. Many arteries, like those of the extremities, are accompanied by more than one vein, and some, like the brachial and spermatic, have more than two; the superficial veins, further, have no corresponding arteries. Nevertheless, any estimate of the capacity of the venous system as compared with that of the arterial can be only approximate, since the quantity of blood flowing

[1] An Experimental Inquiry on some parts of the animal structure, pp. 49, 73, 96, 159, 179, 212. London, 1740.

[2] Researches, Physiological and Anatomical, Vol. i., p. 441.

[3] Elementa Physiologiæ, Tomus I., p. 133.

through the veins must vary according to the pressure and velocity of the flow, the amount passing through the capillaries, the state of the digestion and respiration, etc. Indeed, the most striking characteristic of the venous system is the variability of the amount of blood it contains.

One of the most important features of the venous system is the numerous anastomoses between the veins, which, it will be remembered, are exceptional in the case of the arteries. There are always numerous such channels by which the blood finds a ready route back to the heart, so that, if the flow be obstructed in one vein, an equally easy way is offered by another. The anastomoses between the veins are very important, enabling these vessels to accommodate themselves to the great variation in the quantity of blood flowing into them to which they are subject. The anastomoses, together with the valves, serve to provide against any obstacle to the freedom of the capillary flow, the importance of which we have already seen. In addition to the anastomotic branches usually described may be mentioned others less well known, such as those connecting the vena cava and portal, the œsophageal and hemorrhoidal, the diaphragmatic connecting the hepatic circulation with the vena cava. The importance of these anastomotic vessels becomes evident when the veins usually returning the blood to the heart are obstructed. Under such circumstances, they become greatly enlarged, as is well known to the pathological anatomist.

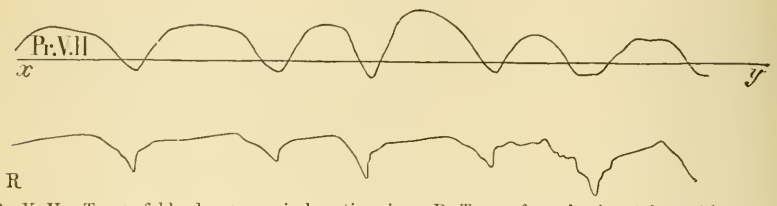
When it is remembered that the arterial pressure gradually diminishes as we recede from the heart to the periphery, it might be expected by the time that the blood has passed through the capillaries and reached the veins, that it would exert but little pressure in the latter. This has been experimentally shown to be the case. Thus, according to Volkmann[1] while the pressure of the blood in the metatarsal artery of the calf was 146 mm. of mercury (5.8 inches) that in the metatarsal vein was only 27.5 mm. (1.1 inch). It has also been shown that as we return from the capillaries to the heart the pressure in the veins gradually falls, the pressure in the femoral vein being 11.4 mm., in the brachial 4 mm., in the facial 3 mm., and in the larger venous trunks near the heart negative. That the pressure in the veins near the heart may be negative, that is less than that of the atmosphere, is well shown by the experiments of Barry.[2] This consists in introducing into the jugular vein of a horse or dog a bent tube, of which the opposite end is immersed in a vase of colored liquor. With each inspiration the liquid rises in the tube, falling again with each expiration. While the pressure is diminished in the jugular and hepatic veins during inspiration, on the other hand, in the remaining abdominal veins it is increased; the latter being compressed by the viscera through

[1] Die Hæmodynamik, s. 173.

[2] Recherches experimentales sur les causes du mouvement du sang dans les veines. Paris, 1825, p. 17.

the falling of the diaphragm, an obstacle is offered to the flow of the blood, and the pressure rises. The lowering of the venous pressure during inspiration is shown graphically by Fig. 161, in

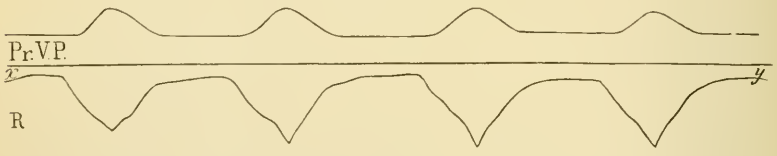
FIG. 161.



Pr. V. H. Trace of blood pressure in hepatic veins. R. Trace of respiration, taken with pneumograph. (MAREY.)

which the depression of the upper trace Pr. V. H, representing the blood pressure, coincides with that of the lower trace R, representing the respiratory movement. The increase in the pressure in the abdominal veins during inspiration is well shown by Fig. 162, in

FIG. 162.



Pr. V. P. Trace of blood pressure in portal vein. R. Trace of respiration, taken with pneumograph. (MAREY.)

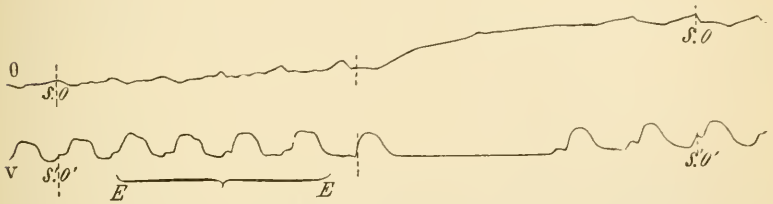
which the depression in the lower trace R, due to inspiration, coincides with the elevation of the upper trace Pr. V. P., due to the increase in the blood pressure. On the other hand, during expiration, the pressure in the abdominal veins is diminished, since the viscera no longer compress these vessels, the diaphragm being elevated. If, however, the expiration be violent, then the contraction of the abdominal walls compresses the viscera and the veins and increases the pressure.

The weight of the blood influences the pressure in the veins. Thus, the blood flows more readily to the heart in the veins of the upper extremity when the limb is elevated than when hanging down. The varicose condition often observed in the veins of the lower extremities illustrates the effect of the venous pressure due to the weight of the blood. While the pressure in the veins is ordinarily very slight, at times it is so much increased as to give rise to a pulsation—the venous pulse. This may be due to an obstruction in the veins, or to an increase in the quantity of blood flowing in these vessels. Thus, if all the venous blood in a part be forced to return to the heart by a single vein, as can be effected by ligating all the adjacent veins, as in the experiment of Poisseuille,[1] the pres-

[1] Magendie, Leçons sur les phenomenes physique de la vie, Tome iii., p. 181. Paris, 1837.

sure on the vein will be so much increased as to equal that of an artery of like size, the force of the heart being exerted upon the blood of a single vein, and therefore concentrated instead of as ordinarily upon several and, therefore, diffused and dissipated. During the ventricular systole, and, therefore, when the tricuspid valve is closed, the flow of the blood through the auricle into the ventricle is, for the instant, stopped, the pressure in the auricle and vena cava is then momentarily increased. If, however, the beating of the heart cease in diastole, as in the case after excitation of the pneumogastric nerve, the blood will flow into the ventricle, which, being filled, receives then no more blood from the auricle; the blood continuing to flow will fill the auricle and the vena cava until these parts, being distended, the pressure will be very much increased. This can be experimentally shown in the frog by means of the double myograph. By comparing the traces (Fig. 163) of

FIG. 163.



O. Trace of auricle. V. Trace of ventricle. *S' O.* Systole of auricle. *E.* Stimulation of the pneumogastric nerve. (MAREY.)

the auricle and ventricle, taken simultaneously, it will be observed that the pressure in the auricle is increased during the arrest in diastole of the heart's action through stimulation of the pneumogastric nerve.

There is also observed at times in certain veins, the external jugular, for example, a regurgitant venous pulse. This is due to a reflux of blood from the right side of the heart, and is synchronous with the movement of expiration, there being no obstacle at the mouth of the vein to the return of the blood if the expiratory movement be exaggerated. It is usually evidence of insufficiency of the tricuspid valve or some other pathological condition. We have seen that the veins are both larger and more numerous than the arteries, and as the volume of blood which passes in a given moment through any part of the vascular system is the same, it follows that the blood ought to flow more slowly through the veins than the arteries. If the venous system be considered twice as capacious as the arterial, then the blood should flow half as slowly through the veins as the arteries. Experiment is in harmony with theoretical considerations, it having been shown by Volkmann [1] that the blood flows in the jugular vein of the dog at the rate of 225 mm. (9 inches) in a second, that of the carotid artery in the same

[1] Op. cit., s. 195.

animal being 329 mm. (13 inches). The velocity of the blood current differs, therefore, from that of the pressure, since the velocity lost in the capillaries is regained somewhat in the veins, whereas the pressure falls continuously, the pressure of the capillaries being less than that of the arteries, but greater than that in the veins. The conditions that influence the rapidity of the flow in the veins, however, vary, so that it is impossible to fix upon any average rate.

There can be no doubt that the flow of the blood in the veins is essentially due to the contractile force of the heart. Thus, according to Sharpey,[1] the hepatic veins can be filled with an injection of defibrinated blood thrown into the aorta under a pressure of 3.6 cm. (1.4 in.) of mercury, which is only about half that of the normal arterial pressure. The experiment of Magendie,[2] in which the femoral vein was ligated and opened, the blood jetting forth, the jet and flow gradually ceasing with compression of the femoral artery, proved the competency of the heart to force the blood through the capillaries into the veins, the force of the artery causing the jet from the vein being, as we have seen, only the reaction from its previous distention, due to the preceding ventricular systole. While the heart is the main cause of the venous flow, as in the case of the capillaries, there are other causes which assist in promoting this movement. Thus, muscular contraction, by compressing the veins, forces the blood in these vessels toward the heart, regurgitation being impossible through the action of the valves. Hence, the significance of the fact of valves being so much more numerous in the veins of the muscles than in the cavities of the body, the veins in the latter situation not being subjected to the same kind of compression as those between and within the muscles. It must be mentioned, however, in order that too much stress be not laid upon this connection between muscular action and the presence or absence of valves, that in some cases, as in the portal vein of the horse and in the mesenteric veins of the reindeer, for example, valves do exist. In order that muscular contraction shall assist the flow of the blood through the veins, not only must valves exist to prevent regurgitation, but the contractions of the muscles must be intermittent, as during the period of repose after a contraction the vein has time to fill up again with blood that will be forced forward with the following contraction. This alternate filling up and emptying of the muscular veins is also of advantage from a nutritive point of view, since, as we shall see, the activity of the muscle depends upon the free and rapid circulation of the blood through its substance.[3] The influence of muscular contraction in accelerating the venous flow is well known to every surgeon, the jet from a vein increasing in force with the contraction of the muscles below the opening. The amount of increase of pressure in the veins, due to muscular

[1] Todd and Bowman, Phys. Anat., 1856, Vol. ii., p. 350.
[2] Journal de Physiologie, 1821, T. i., p. 3.
[3] Milne Edwards, Physiologie, Tome iv., p. 310.

contraction, can be experimentally determined by placing a vein in communication with a mercurial manometer, and observing the variations in the height of the mercury due to muscular contraction, whether produced naturally or by movements of the animal, or induced by stimuli. In the experiments of Magendie [1] and Bernard [2] the mercury rose 50 mm. (2 in.) above the normal venous pressure after a general muscular contraction. However important muscular action may be in promoting the flow of venous blood, that it is not indispensable is shown by the fact that the blood flows through the veins in parts that are paralyzed. When we come to study the mechanism of respiration it will be seen that the thoracic walls alternately expand and contract synchronously with the fall and rise of the diaphragm in the production of the inspiratory and expiratory movements. It will become apparent, then, that the rarefaction of the air within the thorax during its dilatation, which causes the entrance of the external air into the trachea and the lungs in inspiration, must exercise a similar suction influence upon the blood flowing in the large and extensible veins emptying into the heart. This action of the thoracic walls will have, however, little or no influence upon the blood of the aorta, its walls being too resisting to give to any extent. The suction force thus exerted by the thorax during inspiration upon the venous blood flowing toward the heart extends also, to a certain extent, to the veins situated outside of the thorax. The fact already alluded to, of the walls of the superior vena cava, jugular, subclavian, etc., adhering to the surrounding tissues by aponeurotic layers, and so being kept open, evidently favors the flow of the blood through these veins toward the heart during inspiration. Were it not for such a disposition the veins would entirely collapse through atmospheric pressure. The hepatic veins also adhere to such an extent to the tissue of the liver that when divided they remain open, and the inferior vena cava, in which these veins terminate, is further surrounded by fibrous expansions, which fix it to the margin of the diaphragm through which it passes on its way to the heart. The anatomical relations of the parts are such, therefore, as to favor the flow of the venous blood from the liver toward the heart during the contraction and consequent fall of the diaphragm incidental to inspiration. That such a suction force is really exerted upon the venous blood during inspiration by the thorax is seen whenever a violent inspiratory effort is make. At such times the veins at the lower part of the neck are seen to empty themselves completely. The experiment of Barry, already described, illustrates the power of this suction force, the fluid being sucked up into the glass tube introduced into the jugular vein with each inspiration. Barry, however, exaggerated the influence of this suction force. That it does not ordinarily extend much beyond the thorax can be proved by introducing the glass into the

[1] Op. cit., Tome iii., p. 162.

[2] Lecons sur la Phys. et Path. du Systeme Veneux, Tome i., p. 285. Paris, 1858.

anterior end of the jugular vein, when little or no variation will be observed in the level of the liquid with the inspiratory effort.

Death from the entrance of air into the veins is due to the suction force exerted by the thorax during inspiration. The consideration of such cases belongs to pathology, but it may be mentioned here incidentally that the cause of death is due to the blood becoming frothy or spumous when mixed with air, and in that condition will not circulate through the pulmonary capillaries, hence the left side of the heart is found on post-mortem examination empty.

It might naturally be supposed that, as inspiration favors the flow of the venous blood toward the heart, the expiration would oppose it. Were expiration due solely to the contraction of the thoracic walls, such would be, at least to a certain extent, the case, but, as we shall see, the air is expelled during expiration from the lungs to a great extent through the elasticity of the organs themselves, and, as Milne Edwards[1] suggests, this action of the lungs, so far from compressing the veins near the heart, tends to dilate them. A part of the pressure due to contraction of the thoracic walls that would otherwise compress the veins, is, therefore, neutralized by the elasticity of the lungs. It can be shown experimentally by the manometer, as the above consideration would lead us to expect, that the effect due to inspiration upon the flow of the venous blood far exceeds that of expiration. The valves, further, while offering no obstacle to the flow of the blood during inspiration, prevent, to any extent, regurgitation during expiration. Thus, if the manometer be placed in the internal jugular vein above the valves, the effect of inspiration is the same as when placed below them, but in the first case the reflux during expiration amounts to nothing. If expiration be violent, however, then the reflux may be considerable; thus the veins of the neck during singing or prolonged speech are seen to swell up, and when any effort is made in which the glottis is closed. The dilatation of the thorax has but little effect upon the blood flowing in the great veins of the abdomen on account of the flaccidity of their walls, but the diaphragm falling during inspiration compresses the viscera, and they in turn pressing upon the vena cava and its branches, force the blood toward the heart, regurgitation toward the extremities being prevented through the closing of the valves. With the rise of the diaphragm the pressure upon the vena cava will be relieved, and the blood will rapidly flow into it again from the extremities. Should the expiration, however, be labored or violent, and the abdominal walls contract, then the pressure exerted upon the viscera would be an obstacle to the flow of the venous blood from the extremities. In order to appreciate the influences of respiration upon the flow of the venous blood, as seen from what has just been said, we must carefully consider the conditions of the inspiration and expiration, as the same cause may, under different circumstances, produce exactly the opposite effect.

[1] Op. cit., Tome iv., p. 419.

On the whole, respiration favors the flow of the venous blood from the periphery to the heart, and, as we shall see hereafter, the flow of the arterial blood from the heart to the periphery.

The contractility with which the veins are endowed assists somewhat in the lower animals the flow of the blood. This influence is limited in man, however, to the large veins near the heart, and is even there very slight. Gravity, while favoring the flow of the venous blood from parts above the heart, opposes that from below. While muscular action, respiration, contractility, gravity, etc., no doubt at times favor the flow of the venous blood toward the heart, it must not be forgotten that all these conditions are only supplementary to the force of the heart, this being sufficient to force the blood throughout the entire vascular system.

We have seen that the velocity of the blood varies considerably in the different parts of the vascular system, being greatest in the large arteries, least in the capillaries, and intermediate between these extremes in the veins, so far as can be estimated.

There remains now to be determined as far as possible, the general rapidity of the circulation ; that is, the period necessary to complete the entire circuit, or the time that elapses during which a particle of blood passing out of the left ventricle traverses the arterial capillary and venous systems, returning by the right side of the heart and lungs to the point from which it started.

The general rapidity of the circulation can be easily and satisfactorily determined experimentally in a living animal in the following manner, as was first done by Hering :[1] A harmless substance, and easily recognized, is injected into the jugular vein, and blood is drawn as quickly as possible, and at intervals, from the corresponding vein of the opposite side of the head, the time being carefully noted when the substance injected can be detected. Suppose, for example, that a solution of ferrocyanide of potassium be injected into the jugular vein of a rabbit, the salt can be recognized in the blood of the opposite vein in about seven seconds. In this experiment the blood carrying the salt passes to the right side of the heart, then through the lungs to the left side, from there into the aorta, and traversing the capillaries of the head and face returns back by the jugular vein on the opposite side. If the substance be injected into the femoral vein the period elapsing is slightly longer, the vessels through which the blood flows being somewhat longer. This is more evident, however, in a large animal like a horse, than in a small one like a rabbit. Ferrocyanide of potassium is not only used in this experiment on account of it being harmless, but from the readiness with which its presence can be determined in the blood. Vierordt[2] improved somewhat Hering's method by collecting the blood as it flowed at small intervals in little vessels that

[1] Zeitschrift für Physiologie Treviranus, 1829, Band iii., p. 85. Archiv f. physiol. Heilkunde, 1853, Band xii., s. 112 ; 1832, Band v., s. 58.

[2] Die Erscheinungen und Gesetze der Stromgeschwindigkeiten des Blutes, etc., s. 65.

were fixed to a disk which revolved at a fixed rate, the time being determined a little more accurately. The results of the experiments of both these observers, however, agree essentially. According to Hering, the rapidity of the circulation in an animal is inversely as its size, and directly as the rapidity of the action of its heart. Thus, while in the rabbit we have seen that the circulation from jugular to jugular is accomplished in 6.9 seconds, in the goat, dog, and horse, 12.8, 15.2, and 27.3 seconds are required respectively.

If it be assumed that at each ventricular systole 180 grammes (6.4 ounces) of blood are ejected into the aorta and that the heart beats 72 times per minute, it follows that during that time 13 kilogrammes (28 pounds) of blood will pass through the heart. If, however, the blood in the body amounted, for example, to only about 7.2 kilogrammes (16 pounds), it is obvious that less than one minute (about 32 seconds) would be required for all the blood to pass through the heart ($13 : 60 :: 7 : x = 32.3$), an estimate which agrees closely with that determined by experiment in the horse. The only objection to this manner of determining the time required for the whole mass of the blood to pass through the heart is the uncertainty as regards the exact amount of blood in the body, and of the quantity expelled with each ventricular systole. From the nature of the case these data must be variable; the estimate will be true, however, within limits.

In confirmation of what has just been said in reference to the rapidity of the general circulation, etc., it may be mentioned that the time elapsing between the introduction of a poison into the blood and its characteristic effects is about the same as that observed in the experiment of Hering.

Résumé of the History of the Discovery of the Circulation of the Blood.

The discovery of the circulation cannot be attributed to the work of any one man, but to that of many, extending over a period of more than two thousand years. Harvey, with whose name the discovery of the circulation is invariably associated, and justly so, must, however, share the honor with those who preceded as well as with those who followed him, for, on the one hand, the pulmonary circulation was discovered by Servetus and Colombo before Harvey was born, and, on the other, the capillary circulation was not discovered by Malpighi until after Harvey died. To the apprehension of the author[1] at least the discovery of the circulation is marked by six well-defined epoch-making periods, viz.:

1. The structure and functions of the valves of the heart. Erasistratus, B. C. 304.[2]

[1] H. C. Chapman, History of the Discovery of the Circulation of the Blood. Phila., 1884, p. 54.

[2] Claudii Galeni, Opera Omnia, Venetiis, 1556.

2. The arteries carry blood during life, not air. Galen, A. D. 165.[1]

3. The pulmonary circulation. Servetus, 1553.[2]

4. The systemic circulation. Cæsalpinus, 1593.[3]

5. The pulmonary and systemic circulations. Harvey, 1628.[4]

6. The capillaries. Malpighi, 1661.[5]

While it is true that Harvey did not demonstrate the circulation of the blood, never having seen the capillaries, he saw the blood circulating in the mind's eye for he argued that more blood passes through the heart in a given time than can be accounted for by the quantity of the blood in the vessels; hence the blood must pass and repass through the heart, and in estimating the amount of blood flowing from the left ventricle into the aorta during a short period of time even, the same blood must necessarily be counted over and over again.

Again, after noticing the pulsating heart in the snake as it appeared after the animal had been opened, Harvey calls attention to the fact that if the vena cava be compressed it gradually empties itself between the point of compression and the heart; whereas, if the aorta be compressed, it becomes distended between the heart and the point of compression, showing conclusively that the blood in the vena cava flows from the periphery towards the heart, whereas the blood flows in the aorta from the heart towards the periphery. If the great classic of Harvey contained nothing more than the arguments just advanced, they alone would have sufficed to have established the doctrine of the circulation, even though Harvey was obliged to assume, to complete his theory, that the blood passed from the arteries to the veins by anastomosis of vessels or by porosities of the flesh and solid parts that are pervious to the blood[6] the capillaries not having been then discovered.

[1] Galenus, Ebenda, cap. 6.

[2] Christianismi Restitutio, MDLIII.

[3] De Plantis Libri, Florentiæ, 1583, Lib. 1, Cap. II., Quæstionum Medicarum, Venetiis, 1593, Lib. II.

[4] Exercitatio anatomica de motu cordis et sanguinis in animalibus, Francofurti, MDCXXVIII. Prelectiones Anatomiæ Universalis, London, 1886.

[5] Opera Omnia, Lug Bat, 1687.

[6] "Aut anastomosin vasorum esse, aut porositates, carnis & partium solidarum, pervias sanguini esse." Harvey, Exercitatio, Cap. xi., p. 51.

CHAPTER XX.

RESPIRATION.

We have seen that all vital activity is accompanied by waste, that mental, muscular, and secretory action, and the production of animal heat, involve the development of carbon dioxide, urea, etc. Such principles produced through the decomposition of the food and tissues, if retained in the system soon cause death, hence the necessity of their being eliminated; excreted. As the degree of vital activity is conditioned by that of the cell, of fermentation, oxidation, etc., and as it is through respiration that oxygen is absorbed, and carbon dioxide exhaled, it is evident that this function is both absorbing and excretory in character, and must constitute a most important part of nutrition. As might be expected, therefore, the absorbing of oxygen and elimination of carbon dioxide are not necessarily limited to any part of the body, but may go on in every part of it. Further, while the carbon dioxide excreted is, to a considerable extent, due to the combination of the oxygen absorbed with the carbon of the body, there is no reason to suppose that the carbon dioxide excreted at any one moment is produced through the combustion of the oxygen supplied by the air inspired at that moment. On the contrary, the oxygen may have been locked up in the tissues, and supplied, not from the lungs, but from a different part of the economy altogether. In fact, an animal will exhale carbon dioxide in an atmosphere of hydrogen. Under such circumstances, the oxygen of the carbon dioxide must have been absorbed at some previous period.

In the widest sense of the term respiration may then be considered as the process by means of which oxygen is absorbed by the system, and carbon dioxide is excreted, whatever may be the source of the latter. It is often said that, while animals inhale, plants exhale oxygen, and that animal and vegetable life stand, therefore, in a complementary relation to each other. In one sense this is true, since green plants under the influence of solar light decompose carbon dioxide and water, giving up the oxygen and appropriating the carbon, elaborating the latter into starch, fat, cellulose, etc. Animals, on the other hand, through the absorption of oxygen, burn the carbon of their food produced by plants, and exhale carbon dioxide. This antithesis between plant and animal life exists, however, only so long as the plant is regarded as the means by which inorganic matter is combined in a form suitable as nutriment for the animal. When, however, the remaining phenomena of plant life are considered, such as the germination of the seed, the expansion of the

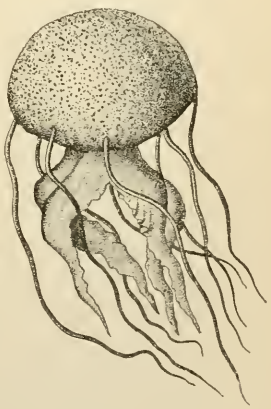
leaf, the budding and flowering, the movement of the sap, it will be found that all such depend upon the absorption of oxygen, and cease when the plant is deprived of it. Respiration, therefore, is as important a function in plant as in animal life.

The phenomenon of respiration or breathing in animals is usually associated with the presence of specialized organs, like lungs, gills, etc. Such structures are, however, not indispensable for the performance of this function, since the muscle of a frog, when separated from the animal and drained of its blood, will absorb oxygen and excrete carbon dioxide as long as the muscle retains its irritability. There are, indeed, two kinds of respiration, an internal one, taking place in all parts of the body, the tissues giving up to the blood the carbon dioxide generated in them, and absorbing oxygen from it, and an external one, the blood giving up to the atmosphere through the lungs or skin its carbon dioxide and receiving oxygen. It is the latter form, or external kind of respiration, ordinarily known as breathing, that we propose considering more particularly at present.

A respiratory organ consists essentially of a membrane separating tissue or blood, containing carbon dioxide, on the one hand, from the atmosphere, or some other medium containing oxygen, on the other; the membrane being of such a character as to permit of osmosis.

It may be mentioned in this connection that a convenient method of illustrating the osmosis of carbon dioxide and oxygen through a membrane is to immerse a pig's bladder filled with venous blood in a bell-jar of oxygen, the carbon dioxide readily passing through the membrane into the oxygen, and the latter in the reverse direction into the venous blood.

Fig. 164.



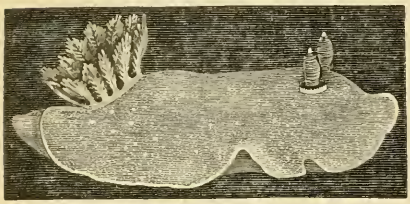
Jelly fish.

Whether the animal be aquatic or terrestrial, simple or complex, the respiratory organs are only modifications of this simple membranous type of structure, and this will be found to be true, as they appear in the form of skin, gills, tracheæ, or lungs. Thus, in many of the lower forms of life, as in the hydrozoa and actinozoa, of which the jelly fish (Fig. 164) and anemone are familiar examples, simply formed animals, in which the differentiation of the functions, or the division of labor is not carried to any great extent, respiration is effected by the general cutaneous surface, the skin readily permitting an exchange between the oxygen dissolved in the sea-water and carbon dioxide developed within their bodies.

In many animals such as the Mollusca (Fig. 165), fishes, perenni-

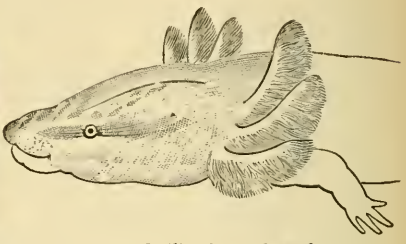
branchiate batrachia (Fig. 166), the respiratory organs assume the form of gills, delicate membranous-like structures, whose thin walls readily permit of an osmosis between the oxygen of the surrounding water and the carbon dioxide of the blood.

Fig. 165.



Doris Johnstoni, showing the tuft of external gills.

Fig. 166.



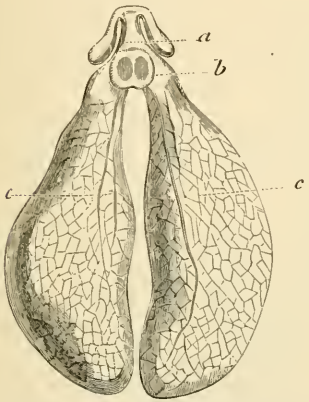
Head and gills of menobranchus.

Another form of respiration is the tracheal. This is seen in insects, centipedes, etc., and consists of innumerable delicate membranous branching tubes or tracheæ, ramifying throughout the entire body of the animal, and which, opening externally by lateral apertures, the spiracles or stigmata, permit the entrance of the air. Finally in batrachia, reptiles, birds, and mammals, including man, respiration is effected by the skin and lungs. The action of the skin as a respiratory surface will be considered with its other functions, and before describing the lungs in man, let us consider a more simple type of lung—that of the frog, for example.

The lungs of the frog (Fig. 167) consist of two vascular bladder-like sacs, communicating directly by short bronchi, or rather bronchial openings, with the larynx. On opening the lung the inner surface (Fig. 168) will be seen to be more or less honeycombed, and the alveoli subdivided into still smaller spaces, or cells. These cells all communicate with the central pulmonary cavity, and are lined with a capillary network intermediate between the arterioles running along the attached borders of the septa and the venules along the free borders. It is evident that a far greater extent of vascular surface is exposed to the air, by this segmented or honeycombed disposition of the inner surface, than if the latter was smooth. If the lungs of the frog be now compared with those of a lizard or turtle, the only noticeable difference is that this segmentation of the lung is more marked, while in birds and mammals it is carried to such an extent that each lung consists essentially of an immense number of these honeycombed sacs subdivided into cells, the extent of the vascular space exposed to the air being, therefore, enormously increased. The respiratory organs in man, in the widest sense of the term, include the nares, mouth, pharynx, larynx, trachea, lungs, thorax, and appropriate muscles. That the nares, not the mouth, constitute the natural entrance for the air to the lungs is shown by the fact that in certain mammals breathing

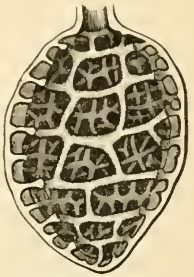
is accomplished through the nares alone. Thus in the cetacea, of which the whale, dolphin, porpoise, etc., are examples, the soft palate is very much developed and so disposed to embrace the glottis and maintain the cavity of the larynx in communication with the posterior nares, a free passageway, however, being left on either side for the food. Such a disposition of the parts makes it possible for the elephant to use its nose or trunk, pharynx and larynx as a siphon to suck up its drinks and transfer the same to the mouth, at the moment that the latter is open the posterior nares communicating with the glottis only. In the horse, camel, etc., the soft palate is also well developed, and surrounds the large epi-

FIG. 167.



Respiratory organs of a frog, as seen on their interior surface. *a*. Hyoidean apparatus. *b*. Cartilaginous ring at the root of the lungs. *c*. Pulmonary sacs, covered with vascular ramifications. (DALTON.)

FIG. 168.



Lung of frog, showing its internal surface. (DALTON.)

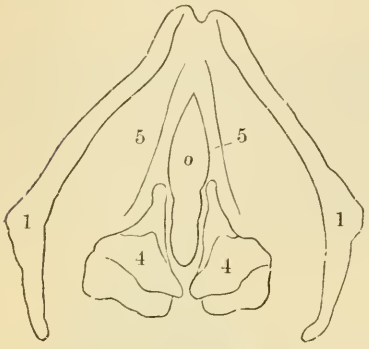
glottis to such an extent as to cut off completely all communication between the mouth and the pharynx, except at the moment of deglutition. Indeed, in the horse, if the facial nerves which supply the muscles of the external nares be divided, the animal dies from asphyxia.

In describing the structure of the hippopotamus, the author called attention [1] to the fact that when the animal passes under the water, the larynx is so elevated within the pharynx that a continuous passage is offered to the air from the external nares to the lungs, enabling the animal to breathe when almost entirely submerged. A similar elevation of the larynx is seen in the young kangaroo, and to a certain extent, also, in the human fœtus and infant. The ill effects often experienced in breathing through the mouth in a cold, dry atmosphere further prove that the natural entrance to the respiratory tract is the nose, since the air as it passes over the partly ciliated moist and very vascular and warm mucous membrane lining the nasal cavities absorbs water, and is elevated to the temperature of the body before entering the lungs. The action of the nares in ordinary breathing is not very apparent, but when the

[1] H. C. Chapman, Proc. Acad. Nat. Sciences, p. 130. Philadelphia, 1881.

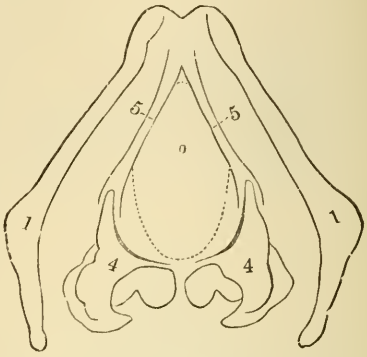
breathing becomes labored, then it is very evident. The air having passed the nose and the pharynx, enters the larynx, a triangular-like structure surmounting the trachea and consisting of sufficiently

Fig. 169.



Human larynx, viewed from above in its ordinary post-mortem condition. 5. Vocal membranes. 1. Thyroid cartilage. 4. Arytenoid cartilages. 0. Opening of the glottis.

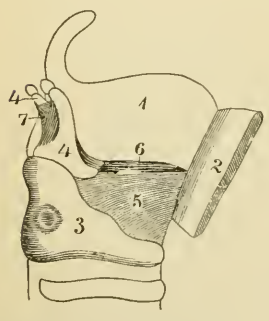
Fig. 170.



The same, with the glottis opened by separation of the vocal cords. 5. Vocal membranes. 1. Thyroid cartilage. 4. Arytenoid cartilages. 0. Opening of the glottis. (Dalton.)

rigid cartilages to resist atmospheric pressure united by ligaments and movable through muscles. The detailed structure of the larynx we will defer till our account of the voice, considering at present only such of its parts as influence respiration. The larynx is lined with mucous membrane, continuous with that of the pharynx; the epithelium, however, except that covering the vocal cords, is of the ciliated, columnar variety, the movement of the cilia being from below, upward. If the larynx be viewed from above (Figs. 169, 170), or in section (Fig. 171), it will be observed that it is divided into an upper and lower compartment by the rima glottidis (0), or the aperture of the glottis, a triangular-like orifice, the sides and base of which are formed by the true vocal cords (Fig. 171) (5, 6) and arytenoid cartilages (4). The vocal cords, or, more properly, the vocal membranes, consist of elastic tissue covered with very thin mucous membrane, and extending from the thyroid cartilages (Fig. 171, 1 and 2) anteriorly, to the cricoid (3), and base of the arytenoid cartilages (4) posteriorly. The upper edges of the vocal membrane extending from the reëntering angle of the thyroid carti-

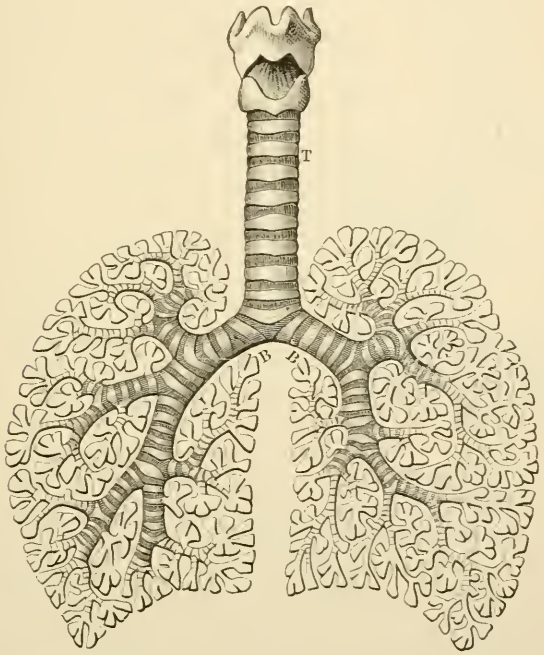
Fig. 171.



View of the vocal membrane. 1. Left half of the thyroid cartilage. 2. Right half turned forward and partly cut away. 3. Cricoid cartilage. 4. Arytenoid cartilages. 5. Right half of the vocal membrane. 6. Upper border of the left half. 7. Arytenoid muscle. The upper borders of the vocal membrane, extended between the arytenoid cartilages and the thyroid, constitute the so-called "true vocal cords." (Leidy.)

lage to the base of the arytenoid are somewhat thickened, and are usually and incorrectly described as separate organs, the "vocal cords." The upper or false vocal cords, so-called because they have no influence in the production of voice, are the thickened upper edges of the ventricle or sac-like pouches extending outward and upward from the larynx between the vocal cords, and lined with the mucous membrane of the same. The glottis or triangular orifice between the vocal membranes and arytenoid cartilages is the passage through which the air from the nose and pharynx enters the trachea and lungs, and during life is alternately dilated and contracted synchronously with the movements of the chest. During

FIG. 172.



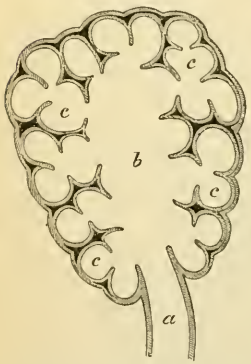
Human larynx, trachea, bronchi, and lungs; showing the ramification of the bronchi, and the division of the lungs into lobules. (DALTON.)

inspiration the glottis (Fig. 170) opens, admitting the air freely to the trachea, while in expiration as the air is expelled upward from below the vocal membranes collapse. These movements constitute the respiratory movements of the glottis and are increased or diminished in intensity in proportion to those of the chest. We shall see that while expiration is usually a passive process, inspiration is an active one, and its tendency is to draw the vocal membranes together. This is provided against, however, through the action of the posterior crico-arytenoid muscles, which arise from the posterior surface of the cricoid cartilage, converge upward and outward, and

are inserted into the base of the arytenoid cartilages. In contracting, these muscles, therefore, dilate at the moment of inspiration the glottis. During expiration, however, these muscles are relaxed, the vocal membranes through their elasticity, and through the contraction of the lateral crico-arytenoid muscles are approximated, and the expired air separates them as it passes upward from the trachea. The importance of the epiglottis covering the larynx during deglutition, and thereby preventing foreign bodies, especially of a liquid nature, from passing into the larynx having been already noticed, it will not be necessary to dwell further upon the function of this structure in its relation to deglutition and respiration.

The inspired air having passed through the larynx enters the trachea (Fig. 172, T), a tube from 10 to 12 cm. long (4 to 4.8 in.) and 21 mm. ($\frac{8}{10}$ in.) in width, beginning at the lower border of the cricoid cartilage above and terminating as the two bronchi below. The trachea consists of 16 to 20 cartilaginous rings, or, more correctly, arcs the posterior third of each ring, being imperfect, deficient in cartilage, the intervening space being filled up with loose fibrous tissue. The cartilaginous rings are connected by a strong fibro-elastic membrane, which so extends over and under them in a thinned condition that they are, as it were, imbedded within it. The last ring of the trachea is somewhat modified in shape, its lower border being brought to a median point so as to accommodate itself to the bronchi. The function of the cartilaginous rings of the trachea is to keep the latter open under varying conditions of pressure. Within the fibrous tissue filling up the posterior third of the cartilaginous rings are found unstriped muscular tissue, the fibers of which are disposed in a transverse, and to a certain extent, also, in a longitudinal, direction. The action of these muscular fibers, sometimes called the tracheal muscle, is to diminish the area of the trachea by approximating the cartilaginous rings, and the ends of each ring, and of so preventing too great distention when the pressure within the air passages becomes very great. The trachea is lined with mucous membrane, its epithelium being of the columnar ciliated character. The motion of the cilia being from below, upward, a current is produced by which the mucus is carried upward toward the larynx.

Fig. 173.

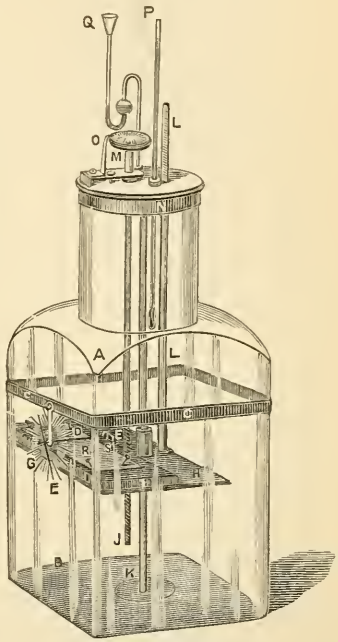


Single lobule of human lung. *a*. Ultimate bronchial tube. *b*. Cavity of lobule. *c*, *c*, *c*. Pulmonary cells, or vesicles. (Dalton.)

Although the cilia are microscopic, varying in length from the $\frac{1}{1000}$ to the $\frac{1}{1600}$ of a millimeter (the $\frac{1}{2500}$ to the $\frac{1}{4000}$ of an inch in length; nevertheless, through their vibratory motion a greater force is exerted than might be expected. The mechanical effect

produced by the motion of the vibratile cilia can be shown by means of the instrument known as that of Calliburcès. This consists (Fig. 174) of a brass stage (H) which can be elevated and depressed on a vertical axis (K) by means of the screw (M), whose movement is graduated. The brass stage supports a cork (I), upon which is horizontally disposed an aluminium rod (D), terminating in an index (F). The brass stage, axis, and disk, etc., are usually covered with a glass cylinder, through which passes a safety tube (S), into which hot water is poured, by means of which the atmosphere is kept moist and the temperature maintained at 28° C. (82° F.). The mucous membrane of the frog, whose cilia are to be examined, having been placed upon the cork (I), before it is covered with the glass jar, is then brought up almost in contact with the aluminium rod (D) by elevating the brass stage (H). When so adjusted, if the membrane be kept moist and warm, the aluminium rod will rotate on its axis through the action of the cilia, the index (F) moving around the graduated circle (G) about once in three minutes for an hour and upwards.

Fig. 174.



Apparatus of Calliburcès.

As the aluminium rod with the index weighs about 0.07 gramme (1.08 grains), it is evident that considerable mechanical effect is produced relatively to the small size of the organs exerting the force. The motion of the cilia of human mucous membrane can often be seen upon the surface of recently extracted nasal polypi when the latter are viewed under the microscope.

The composition of the nasal, as well as that of the bronchial and pulmonary mucus, is shown in the following:

Composition of Nasal Mucus.[1]

Water	993.00
Mucosin	53.30
Sodium lactate	1.00
Organic crystalline principles	2.00
Fatty matters and cholesterin	. . .
Sodium and potassium chloride	5.60
Phosphates	3.50
Sodium sulphate and carbonate	0.90

[1] Robin, Leçons sur les humeurs, p. 450. Paris, 1867.

Composition of Bronchial and Pulmonary Mucus.[1]

Water	955.520
Mucosin	23.754
Watery extract	8.006
Alcoholic extract	1.810
Fat	2.887
Sodium chloride	5.825
" sulphate	0.400
" carbonate	0.198
" phosphate	0.080
Calcium phosphate with traces of iron	0.974
" carbonate	0.291
Silica and calcium sulphate	0.255
	1000.000

The trachea terminates inferiorly in the bronchi (Fig. 172, B, B); the right bronchus differs from the left in being the shorter, attaining, usually, a length of 2.5 cm. (1 inch), while the left is almost twice as long. The general structure of the bronchi corresponds in every way to that of the trachea; the cartilaginous rings are, however, shorter and narrower, and less numerous, the right bronchus consisting, usually, of from six to eight rings, the left of from nine to twelve. Each bronchus divides and subdivides dichotomously into the bronchial tubes (Fig. 172). The latter diverging in every direction, and never anastomosing, gradually become smaller and smaller, and more delicate in structure, and when, finally, they are reduced to about the diameter of the $\frac{1}{5}$ of a mm. ($\frac{1}{125}$ of an inch), they terminate in a primary lobule (Fig. 173). The bronchial tubes differ in several respects from the bronchi, of which they are the diverging branches. Thus, in the larger ones, the cartilages are disposed of as irregular-shaped plates, of various sizes, all over the sides of the tubes instead of in the form of imperfect rings; in the medium-sized tubes the cartilages become smaller and less numerous, while, finally, in tubes having a diameter of less than $\frac{1}{2}$ of a mm. ($\frac{1}{50}$ of an inch) they disappear altogether. The terminal bronchial tubes then consist of a delicate fibro-elastic external membrane, containing circular muscular fibers and a very thin lining of mucous membrane, the epithelium of which is, however, still ciliated. As just stated, each bronchial tube finally terminates in a primary lobule. The primary lobule, with a diameter usually of 2 mm. ($\frac{1}{12}$ of an inch), consists of a sac, which is essentially an expansion of the terminal bronchial tube, hence its name of infundibulum. The cavity of the primary lobule (Fig. 173, *b*) is subdivided by thin partitions, projecting from its inner surface into secondary compartments, the alveoli, or the pulmonary air cells, *c*, *c*, having a diameter of from $\frac{1}{8}$ to $\frac{1}{3}$ of a mm. ($\frac{1}{200}$ to $\frac{1}{75}$ of an inch); these, while separated from each other by the partitions, communicate with the central cavity or intercellular air passages, which, in turn opens into the terminal bronchial

[1] Nasse, Journal of prakt. Chemie, 1843, Band xxix., s. 65.

tube, through which the inspired air ultimately passes to the air cells. The air cells, amounting to 725 millions in number,[1] and representing an area of nearly two hundred square meters (2000 feet), are polyhedral sacs, surrounded by anastomosing elastic fibers, and consist of a fibro-elastic wall, containing, probably, some muscular fibers, and lined with a tessellated epithelium. The epithelium is more homogeneous and easily demonstrated in the fœtus than in the adult. If the primary lobule of the human lung be now compared with the lung of the frog, it will be seen that it represents the entire frog's lung in miniature. The primary lobules of the human lung unite through connective tissue into larger secondary lobules, and the latter uniting, constitute a lung. The polyhedral markings upon the surface of a lung indicate the margins of the secondary lobules, while careful examination will disclose also the outlines of the primary lobules composing the secondary ones. Finally, the integration of the primary lobules into the secondary ones, and the latter into lobes, is carried still further into the left lung than in the right, the former consisting of two lobes, the latter of three. While the lungs are nourished by the bronchi, it is by means of the pulmonary arteries that the venous blood is carried to them from the right side of the heart and aërated. The pulmonary artery arising, as we have seen, from the right ventricle of the heart, soon divides into a right and left branch for either lung. Following the bronchus and bronchial tubes, the artery divides and subdivides, the branches becoming smaller and smaller as they approach the primary lobules (Fig. 175), until finally they terminate as the pulmonary capillaries. The terminal arterial capillaries surround each alveolus or air cell as a vascular circle, which anastomoses with those of the adjacent alveoli. From these vessels arise a capillary network (Fig. 175), so closely set that the meshes are even smaller than the diameter of the vessels themselves, the latter having usually a diameter of from $\frac{1}{80}$ to $\frac{1}{200}$ of a mm. ($\frac{1}{2000}$ to $\frac{1}{5000}$ of an inch). This network supports the bottom of each air cell, and the blood that it carries is separated from the air of the cells only by its wall and the extremely delicate epithelial lining of it. The carbon dioxide of the venous blood conveyed to the lungs by the pulmonary artery is thus separated from the oxygen of the air within the air cells brought by the trachea by nothing but the wall of the capillary and epithelium of the air cell. The rapidity with which the osmosis of these gases takes place through such a

FIG. 175.

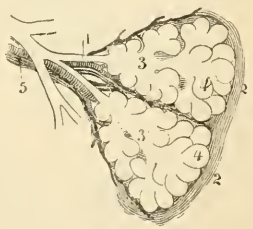


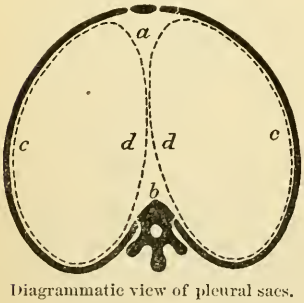
Diagram of two primary lobules of the lungs, magnified. 1. Bronchial tube. 2. A pair of primary lobules connected with fibro-elastic tissue. 3. Intercellular air passages. 4. Air cells. 5. Branches of the pulmonary artery and vein. (LEIDY.)

[1] Landois, op. cit., p. 190.

delicate septum will, therefore, be readily imagined; the osmosis being still further insured through the great vascularity of the parts, the respiratory surface being thereby continually kept moist, which greatly promotes the exchange of the gases.

The full influence of the air upon the blood is further secured in that the capillary plexus is so disposed between the walls of two adjacent air cells that one of its surfaces is exposed to each. It has been estimated[1] that a thin layer of blood of 150 square meters (1500 feet) is exposed in the lungs to the air of the air cells, and that this blood, amounting to perhaps 2 liters (3.4 pints), is renewed 10,000 times in twenty-four hours. This estimate is based upon the assumption that the surface of the capillaries is equal to about three-fourths the surface of the air cells. That this is not an exaggeration may be inferred from the fact of an injected lung appearing to consist of nothing but capillaries. From the capillary network surrounding the air cells the pulmonary veins arise, which, uniting with each other, gradually form four larger trunks, which finally terminate in the left auricle of the heart and convey to it the aërated oxygenated blood to be distributed, as we have seen, by the arterial system to all parts of the body.

FIG. 176.



Diagrammatic view of pleural sacs.

Having described the pulmonary air cells and blood vessels, the passage by osmosis of the carbon dioxide from the blood into the air cells and of the oxygen from the air cells into the blood, let us now consider the means by which the air is drawn into the lungs and expelled from them.

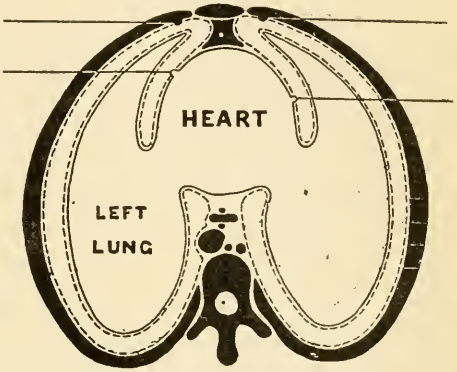
The heart and lungs are suspended by the great blood vessels in the thoracic cavity. The thorax consists of the sternum anteriorly, the dorsal vertebra posteriorly, and the ribs laterally. It is covered in above by the cervical muscles and fascia, below by the diaphragm, and laterally, etc., by the intercostal muscles. The thoracic cavity is therefore air-tight. If the lungs be examined *in sitû* it will be found that the surface of each lung is covered with a serous membrane continuous with that lining the inner surface of the thorax or the pleura. To understand the relations of the pleuræ to the lungs and walls of the thorax, let us first conceive the pleura as consisting of two bladders (Fig. 176), and so placed within an empty thorax that the outer wall (*c*) of each bladder will adhere to the inner surface of the wall of the thorax, the inner walls (*d*) of each bladder remaining free.

Suppose now that the heart and lungs be inserted between the inner free walls of the two bladders, and that each of the latter be made to adhere to the surface of the lung with which it is in con-

[1] Kuss, Physiologie, 1873, p. 338.

tact. Such a disposition being made (Fig. 177) the bladders will then represent the two pleuræ, the inner walls (*d d*) the visceral layer, the outer wall (*c c*) the parietal layers, and the space between the layers the pleural cavities, the spaces between the bladders or the pleura constituting the mediastinal spaces, the narrow septum formed through the union of the two pleuræ the mediastinum. In health the opposed surfaces of the visceral and parietal layers of the pleura are always in contact, there being only fluid enough between them to insure their gliding smoothly over each other. Practically, therefore, in normal respiration there is no pleural cavity. This must necessarily be so, since the thorax being an air-tight cage, as it dilates through the action of the inspiratory muscles and recedes from the lungs, the air within the latter will expand and push the lungs after the receding thorax and so keep the visceral layer of the pleura in contact with the parietal one. The air within the lungs becoming rarefied at the same time through expansion, the external denser air will pass through the trachea into the lungs until the pressure of the air within the latter is the same as that of the atmosphere. It will be observed that while it is the force of the inspiratory muscles that dilates the chest, it is the pressure of the air that expands the lungs, and, further, that inasmuch as the lungs are elastic and therefore offer a resistance to their expansion, the air must overcome this resistance, and hence the pressure exerted by the air within the lungs upon the heart and blood vessels, etc., outside of them must be less than that of the external atmosphere. Thus, suppose, for example, that the pressure exerted by the atmosphere as measured by the barometer be 760 mm. of mercury, and that at the end of a quiet inspiration the pressure exerted by the elastic tissue of the lung amounts to 9 mm. of mercury, then the pressure of the air within the lungs, that is, the intra-pulmonary pressure as exerted upon the blood vessels outside of the lungs would amount to 751 mm. of mercury, the latter, or the intra-thoracic pressure, as it is called, being equal to the difference between the intra-pulmonary and elastic pressures (760 — 9 = 751). It should be mentioned, however, that as the elastic tension exerted by the lungs is proportional to their distention, that is to the depth of the inspiration, the intra-thoracic pressure may be much less than in the example just given, amount-

FIG. 177.



Diagrammatic view of pleural sacs with heart and lungs interposed.

ing to only 720 mm. of mercury during forced inspiration, the elastic tension then being as much as 40 mm. of mercury (760 — 40 = 720). On the other hand as the thorax contracts, and its capacity diminishes, the air within the lungs, exerting now a greater pressure than the air without, will pass out of the lungs, through the tracheæ by which it had just entered the lungs, of course collapsing, their elasticity now aiding the expulsion of the air to the same extent as it formerly opposed its entrance.

After what has just been said it is obvious that the intra-pulmonary pressure or the pressure excited by the air within the lungs is, during inspiration, negative, that is, less than that of the atmosphere, since the external air then passes into the lungs, whereas during expiration it is positive, or greater than that of the atmosphere since the air then passes out of the lungs. On the other hand the intra-thoracic pressure, or the pressure of the air within the lungs, on the blood vessels, etc., outside the latter will be negative, both during inspiration and expiration, since as long as there is any air in the lungs the pressure exerted by it on the outside of the latter will be more or less neutralized by the pressure exerted by the elastic pulmonary tissue. If, however, expiration be forced, as in obstruction of the respiratory passages by violent coughing, for example, the air in the lungs may be so compressed as to exert a pressure upon the blood vessels outside the lungs as suffices not only to neutralize the elastic tension of the pulmonary tissue, thus rendering the pressure equal to that of the atmosphere, but even to elevate the mercury 80 mm. higher and of so making the intra-thoracic pressure positive, or higher than that of the atmosphere. As a still further proof that the lung is pushed out by the air within it and not pulled out by the receding chest wall it may be mentioned that if a hole be made in the chest the lungs will collapse, however forcible the inspiratory movements of the chest may be, since there is nothing to oppose their elastic tension, the atmospheric pressure being exerted equally on both the inner and outer surfaces of the lungs.

The action of the thorax and the lungs in respiration was long ago compared by Boyle[1] to a bellows without a valve, but with a bladder within. According to Boyle, who appears to be the first to have comprehended how respiration is accomplished, the air is drawn into the lungs as the thorax expands just as the air was drawn into the bladder as the bellows dilates and expelled from the lungs as the thorax contracts as the air is expelled from the bladder as the bellows contracts.

The dilatation of the thoracic cavity and the taking in of the air is known as inspiration, the contraction of the thoracic cavity and the giving out of the air expiration, the two acts constituting respiration.

Let us consider now a little more in detail the means by which this alternate dilatation and contraction of the thoracic cavity causing respiration is effected.

[1] Works, Vol. i., London, 1744, p. 64.

CHAPTER XXI.

RESPIRATION.—(*Continued.*)

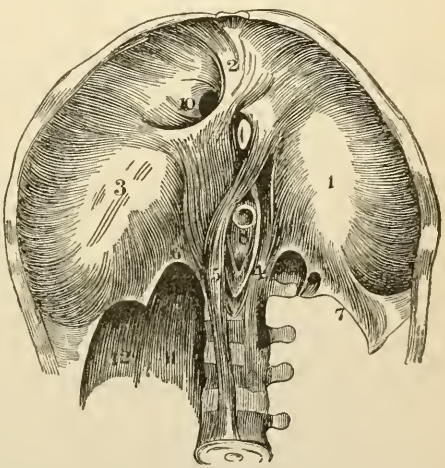
MUSCLES OF RESPIRATION.

Reflection upon the origin and insertion of the various muscles acting upon the thorax makes it evident that some of these muscles in contracting will expand the chest, causing inspiration, while the relaxation of these muscles, together with the elasticity of the lungs and the action of certain other muscles, will contract it, causing expiration. The muscles involved in the production of respiration will then naturally divide themselves into two groups, those of inspiration and those of expiration. To the study of these let us now turn.

Inspiration

Of all the inspiratory muscles the diaphragm is the most important, since the capacity of the chest is enlarged to a greater extent through its contraction than by that of any other muscle. Indeed, in the male sex at least, as we shall see, gentle breathing is accomplished almost entirely by the action of the diaphragm. The diaphragm being attached (Fig. 178), to the ensiform cartilage of the sternum, to the cartilages of the six or seven lower ribs, and often, also, to their osseous portions to the arcuate ligaments and the bodies of the first, second and third lumbar vertebræ, to the invertebral cartilages of the right side, and to the bodies of the first and second lumbar vertebræ, etc., of the left (the crurae) covers in therefore the lower circumference of the thorax. From this origin the diaphragm passes upward into the cavity of the thorax as a vaulted arch or dome (Fig. 179, *B*), the central tendon being the common point of insertion of the muscular fibers which are of the voluntary character. The diaphragm pre-

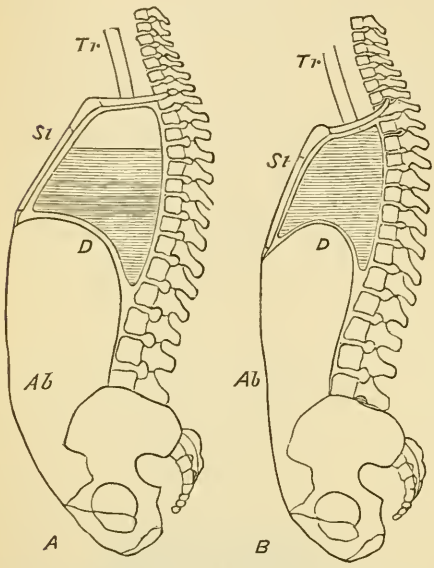
Fig. 178.



Interior view of the diaphragm. 1, 2, 3. The three lobes of the central tendon, surrounded by the fleshy fasciculi derived from the inferior margin of the thorax, the crura, 4, 5, and the arcuate ligaments, 6, 7. 8. Aortic orifice. 9. Œsophageal orifice. 10. Quadrate foramen. 11. Psoas muscle. 12. Quadrate lumbar muscle.

sents several openings through which pass the œsophagus, aorta, vena cava, etc., and is supplied by the phrenic nerve. During the state of repose, as we have just seen, the diaphragm presents the form of a dome or of a vaulted, arched, or curved surface. If the diaphragm, however, be observed during contraction, as can be readily done by opening largely the abdominal cavity of a completely insensible living mammal, a cat, dog, or rabbit, for example, it will then be seen that through the contraction of its muscular fibers the curved surface of the diaphragm assumes more the form of a plane (Fig. 179, *A*), and that the floor of the thorax descends, the cardiac part more particularly from 5 to 40 mm., according to the depth of the inspiration. The effect of the descent of the diaphragm is, therefore, to enlarge in a vertical direction the capacity of the thorax, and to rarefy the air within it. The external air being then denser than that within the lungs rushes into the latter and proportionally distends them in consequence. The diaphragm through its contraction acts then as an inspiratory muscle; it need hardly be added, however, that it is not the diaphragm, but the air, that actually distends the lungs. The author is in the habit of illustrating the action of the diaphragm in respiration by the simple apparatus represented in Fig. 180. This consists of a bell-jar (*a*), the walls of which correspond to the thorax, and in which are suspended the lungs (*LL*), the trachea (2) passing through the air-tight fitting cork. The bottom of the jar is closed in air-tight, with India rubber (5) corresponding to the diaphragm. It is needless to say that there is no such amount of space as (*d*) corresponding to the pleural cavity in the human being in a state of health. Such being the disposition of the parts, by pulling down the India rubber (5) the air within the jar will become rarefied as indicated by the rise of the mercury in the manometer, the lungs *LL* will expand, and the external air will pass into the latter until the pressure is the same as that of the atmosphere. With the elevation of the India rubber the condition of

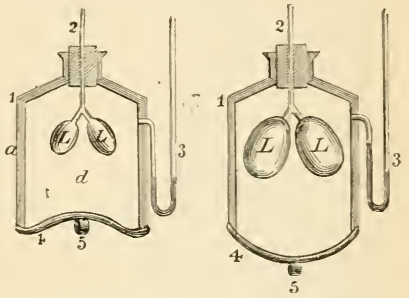
Fig. 179.



Diagrammatic sections of the body in inspiration and expiration. *A*. Inspiration. *B*. Expiration. *Tr*. Trachea. *St*. Sternum. *D*. Diaphragm. *Ab*. Abdominal walls. The shading roughly indicates the stationary air. (Huxley.)

the pressure of the air within and without the jar being reversed, the air will pass out of the lungs, the latter collapsing. As the diaphragm descends it pushes downward and forward the abdominal viscera, and as the anterior and lateral walls of the abdomen are extensible, they give way to the pressure so exerted and are protruded. With each inspiration, therefore, the descent of the diaphragm in man becomes perfectly evident through the movement of the abdomen. The action of the diaphragm in producing inspiration may be readily imitated in man and mammal just dead, by opening the abdomen and pulling the central tendon downward. The external air will rush into the lungs, and often with a distinctly audible sound. While the vertical diameter of the chest is enlarged through the descent of the diaphragm, nevertheless, through the attachment of the latter to the sternum and false ribs, during its contraction through the pulling of the sternum and the upper false ribs downward and inward, and the lower ribs upward and inward toward the vertebral column, there would be a tendency to diminish, to some extent, the capacity of the thorax. This effect is, however, counteracted by the ribs being elevated at the same time as the diaphragm descends, and through the action of certain muscles, to be described later. The elevation of the ribs is such a constant accompaniment of the descent of the diaphragm that in general terms it may be stated that inspiration is effected by the descent of the one, and the ascent of the other, and this is true, even though the breathing appear entirely diaphragmatic.

FIG. 180.



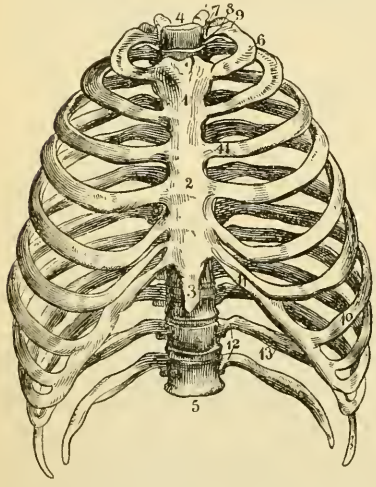
Diagrammatic view of apparatus to show the action of the diaphragm.

The ribs (Fig. 181) pass from their articulations with the dorsal vertebræ downward and forward; they are somewhat twisted in shape and are twelve in number. The upper seven or true ribs are articulated with the sternum; of the remaining five or false ribs, the eighth, ninth, and tenth are joined to the seventh rib, the last two ribs, viz., the eleventh and twelfth, are unattached anteriorly, and are hence known as floating ribs. As the ribs are elevated they recede from each other, the intercostal spaces, with the exception of possibly the first two, being widened. At the same time they are rotated outward, assuming a more horizontal position, and in tending to straighten themselves become less curved. Through their attachment to the sternum the lower portion of the latter is thrown forward, the flexibility of this part of the thorax being mainly due to the sternal attachment of the ribs being cartilaginous and not

osseous. The effect of this change in the form, position, and direction of the ribs and sternum is to enlarge the capacity of the chest in every direction, vertically through the separation of the ribs, laterally through their rotation outward and straightening, antero-posteriorly, through the movement forward of the sternum.

As the external air passes then into the expanding lungs, it is evident that inspiration is produced through the elevation of the ribs as well as through the descent of the diaphragm. The extent of the increase of the capacity of the chest through the elevation of the ribs is greatly influenced by the length, degree of curvature, character of the angles of the ribs, etc. Thus from the ribs being directed obliquely downward and forward when elevated, and assuming a more horizontal position their external ends recede from the posterior wall of the thorax and increase proportionally its antero-posterior diameter. As the ribs are elevated they remain nearly parallel to each other ; it follows, therefore, that the inspiratory effect produced by this movement of the ribs will be proportional to the length, or, more accurately speaking, to the length of the chord of the arc represented by the curve of the rib. This length, however, varies considerably, increasing rapidly from the first to the fifth rib, attaining its maximum at the eighth rib, diminishing then progressively from the ninth to the twelfth. Other things being equal, it follows, then, that the increase in the antero-posterior diameter of the chest is greater at the level of the seventh to the ninth ribs than at the upper or lower part of the thorax. It is for this reason that during inspiration the inferior portion of the sternum moves so much more forward than the upper portion. The transverse diameter of the chest, on the other hand, is greatly influenced by the amount of the curvature of the ribs, and this varies considerably. Thus the curvature increases from the first to the third ribs, the maximum amount being about that of the sixth ; there is but little difference, however, as regards the curvature of the ribs included between the sixth and ninth. The amount of the curvature can be measured by the versed sine of the arc of the circle represented by the rib, or, what is the same thing, the dis-

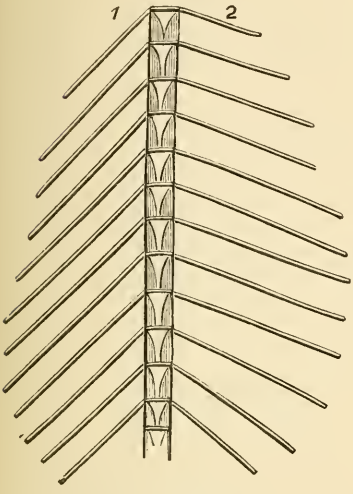
Fig. 181.



Front view of the thorax. 1, 2, 3. The three pieces of the sternum. 4, 5. The dorsal vertebræ. 6. The first true rib. 7. Its head. 8. Neck. 9. Tubercle. 10. The seventh true rib. 11. Costal cartilages. 12. The floating ribs. 13. Groove for the intercostal blood vessels.

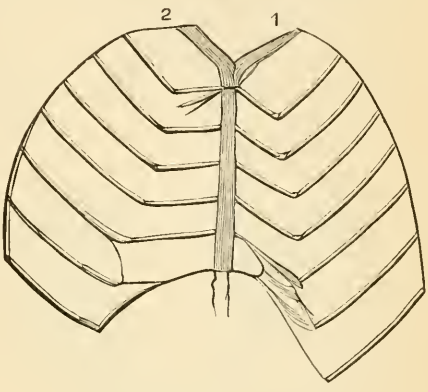
tance from the middle line of the thorax to the most prominent part of it laterally. The angle made by the osseous part of the ribs with their sternal or costal ones, and the length of their car-

FIG. 182.



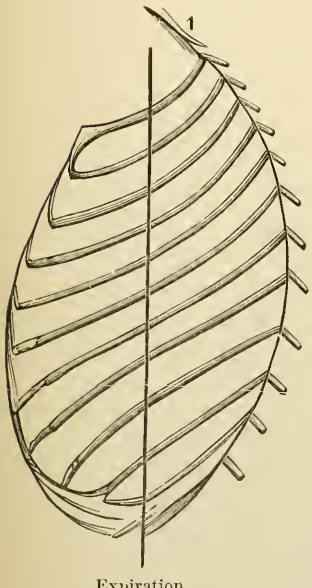
Dorsal region.
Expiration. Inspiration.

FIG. 183.



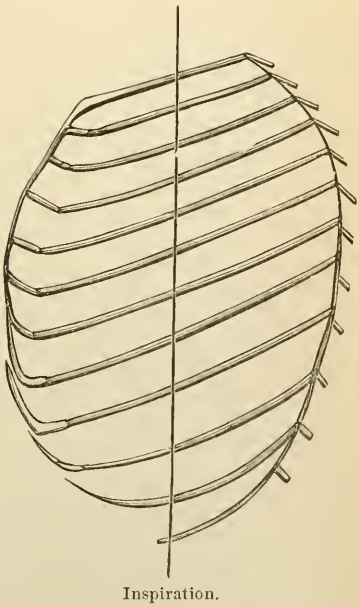
Anterior region of the thorax.
Inspiration. Expiration.

FIG. 184.



Expiration.

FIG. 185.



Inspiration.

tilaginous portions increase from the fourth to the seventh. Consequently, it is in this part of the thorax that the increase of capacity

due to the elasticity and flexibility of the cartilage is greatest. The different extent to which the capacity of the thorax is enlarged in its various diameters during inspiration, the influence due to the variation in the length, curvature of the ribs, etc., are shown by the diagrams (Figs. 182, 183, 184, 185) illustrating the admirable and exhaustive work of Sibson.[1] Let us consider now the muscles which elevate the ribs, and so, together with the action of the diaphragm, cause inspiration.

Muscles of Respiration.

Inspiration.	Expiration.
Ordinary.	
Diaphragm	Internal intercostals, osseous portion.
External intercostals.	
Internal intercostals, sternal portion.	Triangularis sterni.
Scaleni	Infra costales.
Levatores costarum.	
Auxiliary.	
Serratus posticus superior . .	Oblique.
Accessorius	Transversalis.
Sterno-cleido-mastoid . . .	Sacro Lumbalis.
Levator anguli scapulæ.	
Trapezius, superior portion.	
Serratus magnus.	
Pectorales major, inferior portion.	
Pectorales minor.	

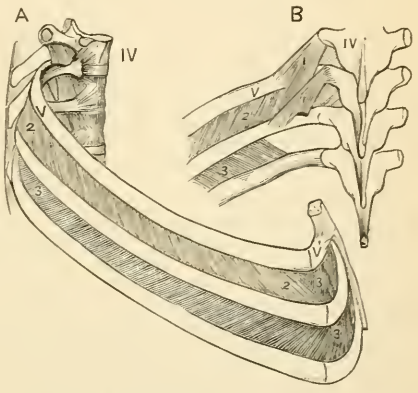
These muscles are usually described as consisting of two sets, ordinary or extraordinary, or auxiliary, according as the breathing due to their action is easy or forced. There is, however, no such sharp line of demarcation observable, it being impossible to say just where ordinary easy breathing ends, and forced breathing begins, great difference being observed in this respect within the limits of health, according to individual peculiarities. There are certain muscles, however, such as the external intercostals, scaleni, etc., which intervene in easy inspiration; these we will consider first, and afterward those coming into play when the breathing is exaggerated. That the external intercostal muscles (Fig. 186, 2) are inspiratory in function one would infer from their attachments, and the direction of their fibers. Passing from rib to rib from above downward, and from behind forward, in contracting these muscles, will approximate and elevate the ribs. Experiment justifies this view of the inspiratory function of the external intercostal muscles, since, if they be exposed in a living animal with each inspiration, they will be seen in contracting to elevate the ribs. Inasmuch, however, as the general direction of the sternal portion of the internal intercostals is also from above downward, and rather forward than backward, through the change in the curve of the rib, analogy would lead us to suppose that their action is the same as that of the

[1] Phil. Trans., 1846, p. 501.

external intercostals, and that they must, therefore, be also regarded as inspiratory in function. This view is confirmed by the observations of Berard,[1] made upon a man in whom the pectoral muscle was so atrophied as to permit of an experimental investigation of the function of the partly exposed sternal portion of the internal intercostal muscle. When the sternal part of the muscle was stimulated, the cartilage of the second rib was elevated, and with it the anterior extremity of the corresponding osseous rib.

The scaleni passing obliquely downward from their origin, the transverse processes of the lower six cervical vertebræ, to their insertion, the first and second ribs, in acting from their origin during contraction will elevate these ribs, and indirectly the whole thorax. To prove that the scaleni do act in this way it is only necessary to squeeze between the fingers the part of the neck including these muscles to feel them contract with each inspiration. The movement then experienced, the so-called respiratory pulse of Magendie,[2] becomes very evident when the superior part of the chest is much dilated. The action of the scaleni is not only to elevate the ribs, but to fix the first rib as an origin from which the intercostal muscles that elevate the ribs can act. Ordinarily inspiration is also effected by the levatores costarum (Fig. 186) as these muscles, arising from the transverse processes of the twelve dorsal vertebræ, and inserted fan-like into the upper edges of the ribs between the tubercles and the angles in contracting, elevate the ribs. The action of the muscles, which we have just considered, usually suffices to produce easy inspiration. When breathing, however, becomes difficult, labored, or very difficult, then inspiration is aided through the contraction of several muscles, the serratus posticus superior, accessorius, sterno-cleido-mastoid, levator anguli scapulæ, superior portion of the trapezius, serratus magnus, and the pectoral muscles. It is not necessary to dwell upon the anatomical disposition of these muscles to prove their importance in labored inspiration. It is evident that the serratus posticus superior passing from the

FIG. 186.



View of several of the middle dorsal vertebræ and ribs, to show the intercostal muscles (A, B). ½. A. From the side. B. From behind. 1, 1. The levatores costarum muscles, short and long. 2. The external intercostal muscles. 3. The internal intercostal layer shown, in the lower of the two spaces represented, by the removal of the external layer, as seen in A in the upper space, in front of the external layer. The deficiency of the internal layer toward the vertebral column is shown in B. (After CLOQUET.)

[1] Physiologie, Tome iii., p. 269.
[2] Precis élémentaire de physiologie, 2d ed., Tome ii., p. 323.

vertebral column to be inserted into the second, third, fourth, and fifth ribs, will, in contracting, elevate the ribs, that the accessorius, extending from the last cervical vertebræ to the angle of the ribs, will produce the same effect. The sterno-cleido-mastoid acts upon the clavicle and sternum, and the levator anguli scapulæ, trapezius, and serratus magnus, through the scapula. Finally, the upper extremities being fixed, the pectoral muscles, reversing their action, will elevate the ribs, their force under such circumstances acting upon the thorax instead of from it. The serrati postici inferiores and quadrate lumborum muscles are regarded by some physiologists as aiding the muscles just mentioned in deep inspiration; according to others, these muscles are expiratory in character.

Expiration.

Expiration is essentially a passive process, consisting in the return of the thorax to the condition in which it was before inspiration. The ascent of the diaphragm, and the descent of the ribs in diminishing the capacity of the thorax, cause the expulsion of the air, or expiration. The relaxation of the inspiratory muscles is, however, accompanied by the contraction of certain muscles which together with the elasticity of the lungs aids in expelling the air from the chest. Inasmuch as the fibers of the osseous portion of the internal intercostal muscles (Fig. 186) pass from rib to rib in exactly the opposite direction as those of the internal intercostal—that is, from above downward, but backward—we would naturally conclude that in contracting they would depress the ribs instead of elevating them, that their function is expiratory instead of inspiratory. Experiment proves that this view is correct, since, if the osseous portion of the internal intercostal muscles be exposed in a living animal by dissecting off the external ones, they will be found to contract during expiration. This antagonism in the action of the internal and external intercostal muscles may be illustrated by a simple mechanical arrangement known as Hamberger's apparatus, though it was really invented by Bernouilli. This consists (Fig. 187, *A*) of two bars (*a* and *b*), which are attached on the one hand to a long vertical rod (*c*) firmly supported, and, on the other hand, to a short one (*d*). The two bars, the long and the short vertical rods, represent respectively the spinal column, two ribs, and a portion of the sternum. The two bars (*a* and *b*) are maintained in the horizontal position by two elastic bands (*w z* and *x y*), which are so attached that as they pass from bar to bar they cross each other at nearly right angles. The elastic band (*x y*) passing from above, downward and forward, represents the external intercostal muscle, the band (*w z*) passing from above downward, but backward, the osseous portion of the internal intercostal muscle. If the band (*w z*) be removed (Fig. 187, B), there being nothing to oppose the elasticity of the band *x y*, or the external intercostal muscle, the bars or ribs will be elevated. If the band

w z be now replaced, and the band *x y* removed (Fig. 187, *C*), then the bars of the ribs will be depressed, there being nothing to oppose the elasticity of the band *w z*. While the action of the external and internal intercostal muscles in respiration, as we have described them, appears to be capable of demonstration in the living animal and imitated by mechanical contrivances, nevertheless, it must be admitted that the action of these muscles has given rise

Fig. 187.

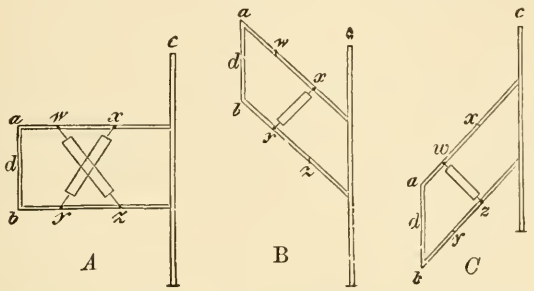


Diagram of models illustrating the action of the external and internal intercostal muscles. B. Inspiratory elevation. C. Expiratory depression. (Huxley.)

to more discussion than that of all the other muscles in the body, and that the most diverse opinions have been offered, and are still held as to their function. Thus, while according to Borelli, Haller, and Cuvier, both the external and internal intercostal muscles are inspiratory, just the opposite opinion, that they are both expiratory was held by Vesalius, Beau and Maissiat Galen. Bartholinus considered the external intercostals to be expiratory, the internal inspiratory, while Spigelius and Vesling held the external intercostals to be inspiratory, the internal expiratory. The external and internal intercostals were regarded at once inspiratory and expiratory by Mayow and Magendie, while according to Arantius and Cruveilhier, both the internal and external intercostals are passive in inspiration and expiration, performing simply the office of a resisting wall in respiration.

Whatever view may be held as to the function of the internal intercostal muscles in respiration, there can be no doubt that the triangularis sterni and infracostalis, and possibly, as already mentioned, the serratus posticus inferior, are expiratory muscles. The triangularis sterni acting from its origin, the ensiform cartilage, the lower border of the sternum, and the lower costal cartilages, in drawing down the cartilages of the second, third, fourth, and fifth ribs must diminish the capacity of the chest. The infracostales produce the same effect, their fibers passing from the inner surface of one rib to the inner surface of the first, second, and third below, their action being from below upward. The muscles that we have just described usually suffice in tranquil expiration; in difficult or

labored expiration, in the acts of blowing, phonation, etc., the muscles entering into the formation of the abdominal walls also come into play. The general effect of these muscles, viz., the external and internal oblique, transversalis, sacro-lumbalis, etc., is in contracting to push up the abdominal viscera and diaphragm into the thorax, diminishing its capacity in the vertical diameter; these muscles, however, in being attached to the ribs or costal cartilages depress at the same time the ribs and consequently diminish the thorax in its antero-posterior and transverse diameters also. The effect of these muscles is, therefore, to aid powerfully in the expulsion of the air from the chest in forced expiration, and as their action and that of the diaphragm is more or less voluntary, and at the same time opposed to each other, the intensity and duration of expiration can, to a great extent, be regulated arbitrarily. The importance of this relation is well seen in singing, in performing upon wind instruments, etc., the skill exhibited depending largely upon the nicety with which the contractions of these muscles can be adjusted to each other.

We have already seen that the lungs are elastic, and were it not for the pressure exerted upon the inner surface of the lungs by the inspired air the lungs would collapse in virtue of this elasticity, and a considerable space in consequence would be left between the lungs and the chest-wall. The natural tendency of the lungs to contract through their elasticity is well seen when air is allowed to enter the pleural cavities. Under such circumstances as already mentioned the atmospheric pressure being exerted equally on both the inner and outer surfaces of the lungs, there is nothing to oppose their elasticity and the lungs therefore collapse. If one end of a tube be passed into the trachea of an animal just dead, and ligated, and the other end be inserted into a water or mercurial manometer, with the entry of air through an opening made into the pleural cavity the lungs will collapse in virtue of their elasticity, the level of the liquid in the proximal end of the manometer will be observed to fall, that of the distal end to rise, the difference in the level of the two indicating and measuring the amount of elastic force exerted. It was in this way that Carson[1] first showed that the elasticity of the lungs in the calf, sheep, or dog would support a column of water twelve to eighteen inches in height, and in the rabbit six to ten inches, and exert a pressure in man amounting to about half a pound upon the square inch.

Finally, the contractility of the bronchi and elasticity of the thoracic walls themselves contribute in expelling the air from the chest. It is usually considered that in inspiration the upper ribs are elevated before the lower, and in expiration the lower ribs are depressed before the upper, the motion being wave-like from above downward and from below upward. According, however, to the observations of Ransome[2] it would appear that the reverse ob-

[1] Phil. Trans., 1820, p. 29. [2] Stethometer, 1876, p. 37.

tains, the lower ribs in inspiration being elevated first and the upper ones last, and that in expiration it is the upper ribs that are depressed first and the lower ones last. Even if such is the case, it is not inconsistent with the view that the upper part of the chest is moved first in inspiration, the lowest last, since if the scaleni act before the intercostal muscles the upper ribs would be elevated before the lower by the action of the scaleni, even if the lower intercostal muscles contracted before the upper. It is possible that the difference of opinion in reference to the order in which the ribs are elevated and depressed is due to the action of the intercostal muscles being considered without reference to the simultaneous action of the other respiratory muscles.

While, in a general way, it can be said that inspiration is due to the descent of the diaphragm and the ascent of the ribs, and expiration to the ascent of the diaphragm and descent of the ribs, nevertheless, there is a noticeable difference, described more particularly by Bean and Maissiat,[1] as to the relative importance of the parts played by the diaphragm and the ribs, as observed in the breathing of the two sexes. Thus while in the male sex breathing is accomplished by the diaphragm and the inferior part of the thorax, or the portion

Fig. 188.

The changes of the thoracic and abdominal walls of the male during respiration.

Fig. 189.

The same in the female. (Hutchinson.)

below the sixth rib, in the female sex it is the superior part of the chest, or that above the seventh rib (Figs. 188, 189), which takes an active part in respiration. It might be supposed that the superior costal type of breathing characteristic of the female is due to

[1] Archives générales de médecine, 1843, 3d ser., t. xv., p. 397 ; 4th ser., 1843, t. i., p. 265 ; t. ii., p. 257 ; t. iii., p. 249.

peculiarities of dress, such as the wearing of corsets, the squeezing of the waist, etc., which would interfere with or prevent even the lower part of the chest expanding.[1] That this is not the only cause, however, is proved by the fact that the superior costal type of breathing prevails even in females that have never worn any kind of clothing whatever. That the superior costal type of breathing is of advantage to the female is obvious when one considers the extent to which the abdominal viscera and diaphragm are pushed up, as is the case during pregnancy, through the enlargement of the uterus. Under such circumstances, if the breathing of the female was of the inferior costal type and diaphragmatic, like that of the male, inspiration would be difficult and labored. It is also on account of this peculiarity in breathing that women can tolerate with so little inconvenience large accumulations of fluid in the abdominal cavity. While in the adult the diaphragmatic inferior costal type of respiration of the male as contrasted with the superior costal type of the female is perfectly evident, the distinction in young children is not noticeable. Indeed, children under about ten years of age breathe almost entirely by the diaphragm. It is not, as a general rule, until near puberty that the distinction in breathing characteristic of the adult sexes becomes apparent. Boerhaave,[2] however, states that the difference in the types of breathing in the sexes in some cases manifested itself as early as the first year.

[1] T. J. Mays, The Therapeutic Gazette, 1887, p. 297.
[2] Prælectiones Academicæ, Gottingen, 1744, p. 144.

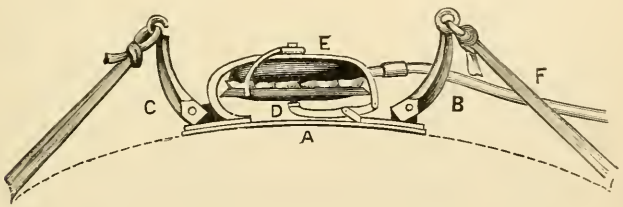
CHAPTER XXII.

RESPIRATION.—(*Continued.*)

RESPIRATORY MOVEMENTS AS STUDIED BY THE GRAPHIC METHOD.

Notwithstanding that the respiratory movements are evident to the eye, and that the respiratory organs can be connected without injury with apparatus for recording their movements, it must be admitted that the application of the graphic method to the study of respiration does not give as satisfactory results as is the case in the study of the circulation. Of the instruments devised for the recording of the respiratory movements graphically, the author has found the pneumograph and stethometer to be among the most useful. The pneumograph, invented by Marey[1] (Fig. 190), consists of an elastic plate A, which is applied to that part of the chest whose

Fig. 190.



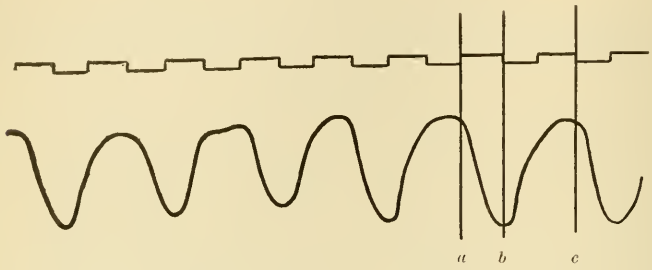
Pneumograph.

movements it is desired to study, and firmly secured there by tapes passing around the neck from the edge of the plate and around the chest from the pillars B and C, projecting from the plate. To the lower end of the pillar B is attached a spring (D), the free end of which is so attached that it presses against the elastic membrane covering in the lower surface of an air-drum (E), the latter communicating through a caoutchouc tube (F), with a recording tambour. With the bending of the elastic plate A through the expansion of the chest, the pillars B and C recede from each other, the spring D ceasing at the same time to press on the membrane of the air-drum E. The air within the drum being therefore rarefied, the air from the recording tambour is drawn into it, and the lever attached to the tambour is depressed. With the contraction of the chest the elastic plate straightens, the pillars approach each other, the spring presses against the elastic membrane, the air is driven out

[1] La methode Graphique, p. 542.

of the drum into the tambour, and the lever is elevated. The depression of lever corresponds, therefore, to inspiration, the elevation to expiration. By placing the lever of the recording tambour in contact with the blackened surface of the cylinder moving by clock-

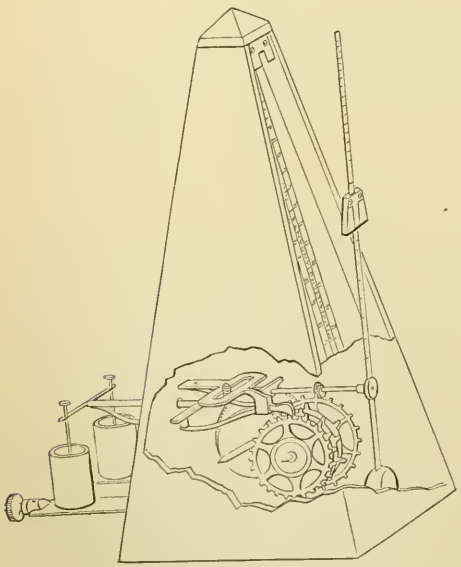
Fig. 191.



Upper line, trace of chronograph. Lower line, trace of respiratory movements. Taken with pneumograph.

work, we obtain a trace like that of Fig. 191, representing the breathing of a man æt. thirty years. In this trace the distance from *a* to *c* represents one respiration; the part of the trace from *a* to *b*, due to the descent of the lever, being inspiratory in origin, that of *b* to *c* due to the ascent of the lever expiratory. It will be observed that the inspiratory movement, as recorded in its trace, *a* to *b*, is extremely abrupt, becoming more gradual at its close, and that the expiratory movement (*b* to *c*) is equally abrupt at the beginning, but that the gradual movement at the termination is more marked even than in the case of the inspiratory movement. In order to determine accurately the number of respirations in a given time, the length of time of one respiration, the relative duration of one inspiration and expiration; the existence of pauses, if any, after inspiration and expiration, it is necessary to make use of some chronographic apparatus, by means of which we can record graphically the time elapsing during which the respiratory move-

Fig. 192.



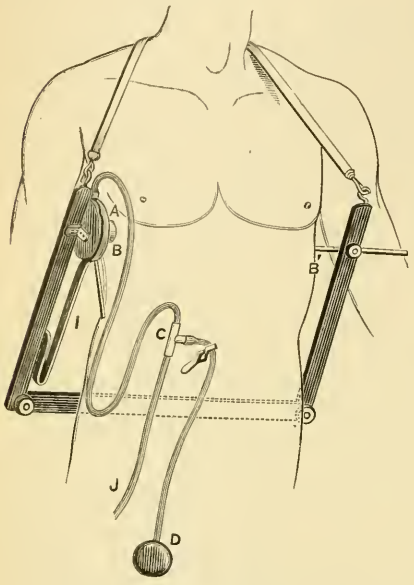
Metronome.

ments are being studied. For this purpose we make use of the metronome in connection with an electro-magnet. The metronome (Fig. 192) is the same as that used by musicians, except that it is constructed that, with each beat of the pendulum a spring is elevated and depressed, to which are attached two needles, dipping into mercury cups. This is accomplished by drawing out or pushing in a rod to which the spring carrying the needles is attached, and which, by so doing, brings the spring in contact with the periphery of either one of four wheels having a different number of cogs. The number of movements of the spring will depend, therefore, upon the particular wheel with whose cogs it is in contact. The four wheels are rotated by the axis common to them, and a fifth one, whose motion is due to an axis, moved by clockwork, which is regulated by a pendulum. With the elevation of the spring the needles are raised out of the mercury in the cups, and with its depression they sink into it again. As the needles are elevated and depressed the current, passing from the battery through the needles and mercury to the electro-magnet, is made or broken, and the marker connected with the latter synchronously depressed and elevated in the manner already described. In the trace obtained by applying the marker of the electro-magnet to the blackened surface of the revolving cylinder as the pendulum beat at the rate of sixty seconds to the minute, the distance between two vertical lines represents one second, and as one respiration was performed in three seconds the number of respirations was twenty per minute, the breathing being more rapid than usual, the average number of respirations throughout the day being from fifteen to eighteen per minute. It will be observed from a comparison of the traces (Fig. 191) that the duration of one respiration was three seconds, the inspiratory part lasting one second, the expiratory two seconds, and that the expiratory lasted, therefore, twice as long as the inspiratory effort; further, that there was no appreciable pause, either after inspiration or expiration, a gradual slowing up of the movement only being noticeable after either. Finally the little undulations of the trace noticeable at the termination of expiration are cardiac in origin.

The object of the stethometer is not only to record the respiratory movements graphically, but to determine also their extent. The instrument consists (Fig. 193) of two parallel bars, the lower ends of which are firmly screwed at right angles into a crossbar so as to form a rigid frame. Through one of the bars passes a slender rod (B′), terminating in a convex ivory knob (B). By means of a screw the extent to which the rod and knob are pushed within the frame can be varied as needed and firmly fixed. The opposite bar carries a spring (I), the upper part of which carries a horizontal pin, terminating at one end in an ivory knob, and at the other in a brass disk, the latter being in contact with the tambour (A) attached to the upper part of the bar. The two ivory knobs not only face each other, but lie in the same axis. The receiving tambour com-

municates by means of the tube J with the recording portion of the apparatus, and also through the T-tube with an India-rubber ball, the latter being used to fill both tambours and communicating tube (D).

Fig. 193.



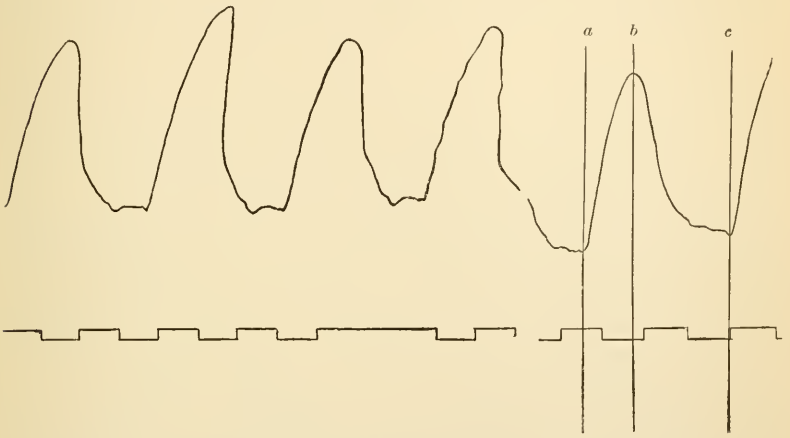
Recording stethometer. A. Tympanum. B. Ivory knob. B'. Rod which carries the knob opposed to B. C. T-tube, by which A communicates, on the one hand, with the recording tympanum, on the other with an elastic bag (D). The purpose of the bag is to enable the observer to vary the quantity of air in the cavity of the tympanum at will. The tube leading to it can be closed by a clip. (Sanderson.)

The manner of adapting the stethometer to the chest will depend upon the part whose movement it is desired to examine. If, for example, we wish to obtain a graphic representation of the movements of the chest in a transverse direction, let the instrument be so applied that the ivory knobs will press upon the eighth rib. The knob being firmly fixed, with the expansion of the chest, the rib will press outwardly the knob of the receiving tambour, the air will be driven out of it into the recording one, and the lever will be elevated; with the contraction of the chest the air will return from the recording to the receiving tambour lever, and the lever will be depressed. With the stethometer, therefore, inspiration corresponds to the elevation of, and expiration to the descent of the recording lever, just the opposite to what happens, as we have seen, when the pneumograph is used. To obtain a trace representing the enlargement of the chest in an antero-posterior direction, the stethometer can be applied so that the ivory knobs are in contact with the manubrium sterni and the third dorsal spine, or the ensiform cartilage and the tenth dorsal spine respectively. Fig. 194 is that of the trace obtained by the stethometer as applied to the seventh ribs in the case of a healthy man, æt. 30 years, and is a graphic representation, therefore, of the respiratory movements, in so far as they depend upon the enlargement of the chest in a transverse direction in that particular part of the chest.

It is not necessary to dwell upon the peculiarities of the trace recorded by the stethometer. It will be observed that the part of the trace from *a* to *b* corresponds to the inspiration, that from *b* to *c* to expiration, and that the relative duration of inspiration to expiration is somewhat different from that observed in the trace obtained by the pneumograph, the number of respirations being in

this case eighteen to the minute. On an average the ratio of inspiration to expiration is as 5 to 6. In order to determine the extent of the enlargement of the chest by the stethometer, the instrument must be graduated. This can be done either by placing successively between the ivory buttons, rods differing by a known length, and observing the different levels to which the lever is elevated, according to the rod used, the vertical distances between the horizontal lines made by the lever corresponding to a definite increase in the distance between the ivory knobs of the particular diameter of the chest examined, or by placing directly underneath the ivory knobs a graduated rod, carrying a vertical slide, which can be pushed against the movable knob, and noticing the different heights to which the recording lever is elevated. In the trace rep-

FIG. 194.



Upper line trace of respiratory movements taken with stethometer. Lower line trace of chronograph.

resented in Fig. 194, the elevation of the lever through the space *a* to *b* corresponds to an increase of about 2 mm. ($\frac{1}{12}$ of an inch) in the lateral diameter of the chest.

While in tranquil breathing the increase in the antero-posterior diameter of the thorax may be only one mm. ($\frac{1}{25}$ of an inch) in forced breathing, according to Ransome,[1] it may amount to as much as 12 to 30 mm. ($\frac{1}{2}$ to 1.2 inch).

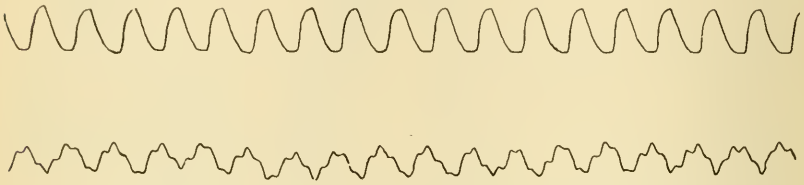
It may be mentioned that the movements of the diaphragm can be studied graphically in an animal by inserting through the ensiform cartilage or the abdominal walls a long probe, so that one end will be in contact with the diaphragm and the other with a recording lever.

In describing the circulation it will be remembered that attention was called to the large undulations present in the curve of blood

[1] Sanderson, Handbook Phys. Lab., p. 302.

pressure, and which at that time were simply stated as being, to a certain extent at least, respiratory in origin. In order to study the influence of the respiration upon the circulation, it is essential that a comparison should be made between the curves of blood pressure and respiration taken simultaneously. In the case of man this can be done by applying at the same time the cardiograph and pneumograph and comparing the traces so obtained, or in an animal by connecting a recording tambour with its trachea, and comparing the respiratory trace so obtained with that of the pressure of the blood in its carotid artery, taken in the manner already described. A comparison of the traces of the respiratory movements and the blood pressure in a rabbit (Fig. 195), taken by the latter method, shows

FIG. 195.

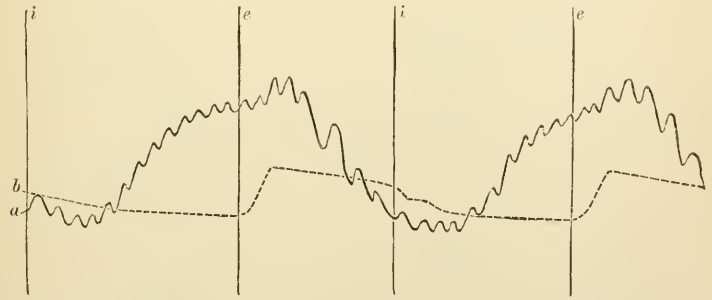


Traces of blood pressure and respiratory movements of rabbit taken simultaneously. Lower trace blood pressure. Upper trace respiratory movements.

that in this case at least the inspiration is almost, if not absolutely, synchronous with the rise of blood pressure and expiration with the fall, the relation between the two naturally suggesting that inspiration is the cause of the one, expiration of the other. Nevertheless, reflection makes it clear that respiration on the whole favors the circulation of the blood even though inspiration promotes it to a greater extent than expiration. Let us consider in detail a little why this must be the case. During inspiration, as the chest expands, the air within the lungs becomes rarefied and the external air passes through the trachea from without inward. In doing this, however, the external air has overcome the elasticity of the lungs, the pressure exerted by the air within the lungs upon the intrathoracic vessels will therefore be that of the ordinary atmospheric pressure, less the pressure due to the elasticity of the lungs. Suppose, for example, that the pressure exerted by the elasticity be half a pound to the square inch, then the pressure exerted by the air within the lungs upon the great blood vessels or the intrathoracic pressure will be only fourteen and a-half pounds, that of the atmosphere being fifteen pounds. The effect of this difference of the atmospheric pressure within and without the chest during inspiration is that a greater quantity of venous blood being forced through the great veins toward the right auricle of the heart and thence through the lungs, a proportionately greater quantity of arterial blood passes, therefore, through the left ventricle into the aorta, the result of which will be to increase the blood pressure. The flow of

the venous blood from the periphery to the heart being promoted by inspiration, it might be supposed that the flow of the arterial blood in the reverse direction would be proportionally retarded. It must be remembered, however, that the pressure exerted by the extrathoracic air upon the thin, flaccid walls of the veins will produce a greater effect than upon the thick, resisting coats of the arteries, and that the pressure of the external air so exerted is not much in excess of the resistance that the heart has to overcome in driving the blood from the ventricle into the arterial system during its systole. During expiration the conditions being the reverse of those obtaining during inspiration the flow of blood through the arteries is favored, since apart from the chest being compressed, the pressure exerted by the intrapulmonary air upon the arteries outside the lungs becomes greater in proportion as the lungs contract, their elastic tension diminishing proportionally. On the other hand, the flow of the blood through the veins is not retarded to any great extent during expiration as the veins are somewhat dilated at the moment of the contraction of the lungs, while regurgitation is prevented by the valves. Respiration on the whole, therefore, favors the circulation, since inspiration aids the flow of the venous blood without offering any great obstacle to the arterial flow, while expiration favors the flow of the arterial blood without retarding to any extent the venous flow, and while it is true that in the influence of respiration upon the circulation, inspiration is more important than expiration, nevertheless the difference in the effect of the two

FIG. 196.

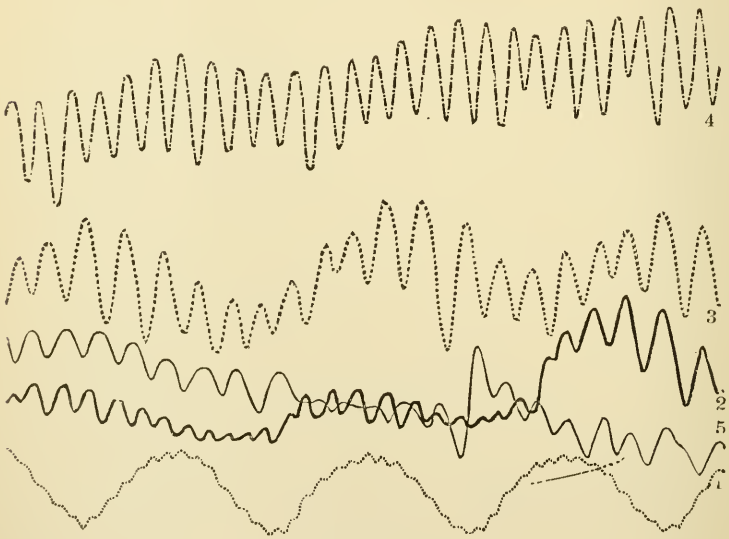


Comparison of blood pressure curve with curve of intrathoracic pressure. To be read from left to right. *a* is the blood-pressure curve, with its respiratory undulations, the slower beats on the descent being very marked. *b* is the curve of intrathoracic pressure obtained by connecting one limb of a manometer with the pleural cavity. Inspiration begins at *i*, expiration at *e*. The intrathoracic pressure rises very rapidly after the cessation of the inspiratory effort, and then slowly falls as the air issues from the chest; at the beginning of the inspiratory effort the fall becomes more rapid. (FOSTER.)

is too small to warrant the conclusion that the large rise and fall in the blood pressure are entirely caused by inspiration, on the one hand, and expiration on the other. Further, in the dog and in the rabbit also, at times, there is no absolute synchronism between the vascular and respiratory rhythms; in the dog, for example (Fig. 196), the rise in the blood pressure lasting not only to the end of

the inspiration, but during a part of expiration, and the fall in blood pressure lasting not only till the end of expiration, but during a part of inspiration. This want of synchronism between the rhythms, together with the fact that the large undulations characteristic of blood pressure persist even after all respiratory movements have ceased, proves that there must be some influence other than respiration concerned in their production. Thus if an animal, a rabbit, for example, be curarized, in which condition the respiratory nerves cease to act altogether, the heart continues to beat, artificial respiration be maintained and a trace of the blood pressure be taken, a curve like that of Fig. 197 will be obtained. If now the artificial respiration be discontinued the blood pressure rises, and the character of the curve changes; nevertheless, a rhythmical rise and fall still occur, like that of Fig. 197. The curve so obtained is known as that of Traube, from having been first described by that observer. Inasmuch as respiration has entirely ceased, it is evident

Fig. 197.



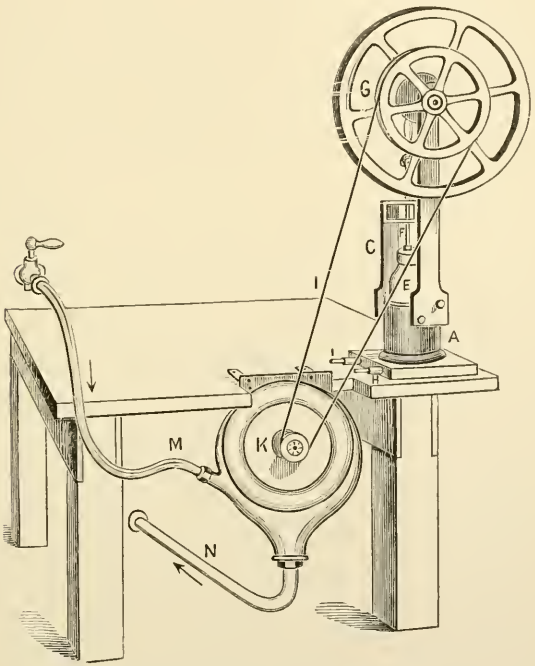
Traube's curves.

that the large undulations cannot be due to respiration. The only way of accounting for them is by supposing that they are of vasomotorial origin, the rhythmic rise and fall in the blood pressure, through the rhythmic constriction of the arteries, being due to a rhythmic stimulus emanating from the vasomotor center of the medulla. This view is confirmed by the following facts: that the phenomena in question are much less marked if the spinal cord be divided below the medulla, and that the undulations persist even after the heart itself be removed, and the circulation be maintained artificially. It is difficult to understand why the vascular rhythm,

due to the vasomotor center, should simulate and be superimposed upon the respiratory rhythm due to the medullary respiratory center, unless through conditions in the evolution of the animal and which we are not familiar with, the two centers in the medulla have been gradually brought to act synchronously. It will be seen, therefore, that while the rise and fall in the blood pressure are influenced by inspiration and expiration, the phenomenon is independent of respiration, or probably that both are influenced by a common cause.

In the study of the circulation and respiration as in the present case it is often necessary to maintain artificial respiration. The form of apparatus that we make use of for this purpose is essentially a mercurial pump (Fig. 198), consisting of two cast-iron

FIG. 198.

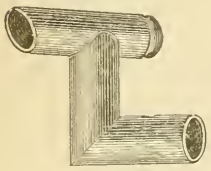


Mercurial pump for artificial respiration.

cylinders A, B (B not being seen in Fig. 198), concentrically disposed and firmly fixed in a solid frame C. The space between the cylinders contains mercury, through which the bell-jar E covering the internal cylinder B is elevated or depressed by the vertical motion of the rod F connecting it with the wheel G, to the rotation of which the motion of the rod is due. The internal cylinder B opens externally through the two brass nozzles H and I. Each of these nozzles is provided with a valve, which, however, open in

opposite directions—that of H from without inward, that of I from within outward. As the bell-jar is elevated the air passes through H into the internal cylinder, and as it descends the air passes out of it through I, and thence by means of a tube terminating in a canula to the trachea of the animal whose respiration is to be maintained. The rotation of the wheel G, to which the action of the respiratory pump is due, is effected by a Backus water motor (K) to which the wheel is connected by the band I. The water supplying the motor is conveyed to it from the hydrant in the laboratory by the tube M and away from it to the waste-pipe by the tube N.

Fig. 199.



Canula.

The canula that we use for insertion into the trachea is that of Ludwig, and consists of a tube of glass (Fig. 199) of which the end *a*, when *in situ*, faces the lungs and through which the air to be inspired passes, the expired air escaping by a small opening.

In ordinary tranquil respiration no sound is heard unless the ear be applied directly to the chest, excepting when the mouth is closed and the breathing exclusively nasal, then a soft murmur accompanies both inspiration and expiration. If the ear, or better, the stethoscope, be successively applied over the trachea and the chest, a very noticeable difference will be observed in the character of the sound heard, as the air passes through these parts both in inspiration and expiration. As might be expected, as the air passes in and out of the trachea, the character of the sound is tubular. In inspiration, the sound, attaining its maximum intensity immediately, maintains it to the close of the act, when it rather suddenly ceases. Immediately, or after a very brief interval, the expiratory sound follows, attaining soon its maximum intensity, but, unlike the inspiratory sound, rather dying away than ceasing abruptly. As the air passes into the small bronchial tubes and expands the pulmonary air cells it gives rise to a sound difficult of description, and which can only be appreciated by being heard. It is usually described as being of a breezy or vesicular character, and is less intense than the tracheal murmur. The sound gradually increases in intensity from the beginning to the end of inspiration, and ceases rather abruptly. The inspiratory murmur is followed without any interval by the expiratory one, lower in pitch, less intense, and lasting a shorter time. It must be mentioned, however, that the expiratory murmur is frequently absent. Certain modifications of the respiratory sounds and movements, such as snoring, coughing, sneezing, sighing, yawning, laughing, sobbing, and hiccoughing need only a passing notice, since they are simply exaggerations of either the inspiratory or expiratory movements, or of both. Snoring, a sound too familiar to need description, occurs when the mouth is open, and is due to a vibration or flapping of the velum palati between

the two currents of air from the mouth and nose together with a vibration of the air itself. Coughing and sneezing, usually involuntary acts, consist in a deep inspiration, followed by a convulsive expiration, differing only in degree, the air in the first instance being expelled by the mouth, in the second by both mouth and nares. Sighing and yawning are due to the same cause—want of oxygen in the blood—and differ from each other only in the former being voluntary, the latter involuntary. In both these acts a prolonged and deep inspiration is followed by a quick and usually audible expiration. Laughing and sobbing, though expressing very different emotions, are produced very much in the same way, and are the result of short, quick, convulsive movements of the diaphragm, which are accompanied by the action of the facial muscles producing those changes in the features so characteristic of joy or sorrow. Laughing and sobbing, like yawning, are, so to speak, catching, or contagious. Hiccough is a purely inspiratory act, and consists in sudden convulsive involuntary contractions of the diaphragm, the glottis constricting spasmodically at the same time; the well-known sound is due to the air striking against the closed glottis. Hiccough is frequently caused by partaking too rapidly of dry food or effervescing and alcoholic drinks, and is not an infrequent symptom of disease.

It is obviously of importance that the number of respirations in a given time be determined as accurately as possible. A great difference of opinion, however, has prevailed, in this respect, among physiologists, Haller,[1] for example, giving twenty respirations a minute as the normal number; Magendie,[2] fifteen; Milne Edwards,[3] sixteen to twenty-two. This disagreement in the result of a mere matter of observation is due, in some instances, to the number of cases examined having been too limited to warrant a general conclusion, and, in others, to influences modifying the number of respirations within the limit of health not having been taken into consideration. The importance of examining a great number of cases before drawing any conclusion as to the average number of respirations per minute is well shown by the observations of Hutchinson.[4] Of 1887 cases, in 561 the number of respirations was found to be twenty per minute; in 239 cases, sixteen per minute; in 79 cases, nine to sixteen per minute. Such a difference in the number of respirations, as observed in these three sets of cases, and also of the remaining ones examined, prove that there must be numerous conditions influencing the rapidity of the respiratory movements as we have seen is the case with the pulse.

Among these the influence of age is very important, thus, as shown by Quetelet,[5] the number of respirations at birth are more

[1] Elementa Physiologiæ, Tomus iii., p. 289.
[2] Précis élémentaire de Physiologie, Tome iii., p. 337.
[3] Physiologie, Tome ii., p. 480.
[4] Cyclopædia of Anat. and Phys., Vol. iv., Part 2, p. 1085.
[5] Quetelet, Sur l'homme, etc., 1835, Tome ii., p. 84.

NUMBER OF RESPIRATIONS PER MINUTE.

Per minute.	No. of cases.	Per minute.	No. of cases.
9 to 16	79	21	129
16	239	22	143
17	105	23	42
18	195	24	243
19	74	24 to 40	78
20	561		

In a total of these 1887 cases the majority breathed 16 to 24; one-third 20 respirations per minute.

than double the number at twenty years of age, and from this age upward the number of respirations diminishes. It is evident, therefore, that the number of respirations per minute, as deduced from the examination of a number of individuals, will depend, *cæteris paribus*, upon their age; and we should expect to find young persons breathing more rapidly than old ones. It will be readily understood, therefore, why 561 persons, on an average, should be

RESPIRATIONS AT DIFFERENT AGES.

Per minute.	Age.
44	At birth.
26	5 years.
20	15 to 20 years.
19	20 to 25 "
16	30 "
18	30 to 50 "

found to breathe twenty times per minute, and 239 persons only sixteen, if the first set of persons examined are, on an average, younger than the second set.

In speaking of the various conditions that modify the number of cardiac beats in a given time, the influence of size was noticed, it being mentioned that the number of cardiac beats in a given time was more numerous in the young and small child, and young and small animal, than in the adult man or large animal. Now, the same relation that we have just pointed out as existing between youth and the number of respirations in man, will also be found to prevail if large animals are compared with small ones, or if the same animal be compared at different ages. Thus, according to Milne Edwards,[1] while the number of inspirations in the whale is only about four or five in the minute, and in the rhinoceros, hippopotamus, giraffe, and horse ten to the minute, the number of respirations are thirty-five or more in the same period of time in the rabbit and guinea-pig, while, according to Colin,[2] the number of respirations being thirteen to sixteen in the sheep, will be sixteen to seventeen in the lamb; in the cow, fifteen to eighteen; in the calf, eighteen to twenty; in an adult dog, fifteen to eighteen; in the young dog, eighteen to twenty. The cause of this difference in the number of respirations, according to the age and

[1] Physiologie, Tome ii., p. 486. [2] Physiologie Comparée Tome ii., p. 152.

size of the animal is, no doubt, due, as in the case of the number of cardiac beats, to the same cause, that of the vital processes generally being more active in small animals than in large ones.

Sex seems to influence but little the number of respirations, no appreciable difference being observed in boys or girls; young men, however, breathe a little more rapidly than young women of the same age. Everyday experience teaches us to what an extent respiration may be accelerated by nervous excitement and exercise. The influence of muscular exertion is not limited simply to active exercise, the mere change from the recumbent to the sitting position, or of standing up, will increase the respiratory movements. Thus, Dr. Guy states that lying down the number of his inspirations was 13 per minute, while sitting 19, and when standing up 22. As might be expected, during sleep, the number of respirations is diminished, according to Quetelet,[1] the diminution being about 1 in 4, or 25 per cent. It will be seen, from what has just been said, that the number of respirations must vary very much within the limits of health; and that, therefore, only an approximately average number can be ascertained. Of 1887 cases examined by Hutchinson,[2] 1731 breathed from 16 to 24 times, and nearly one-third of them 20 times a minute. The average number of respirations we have found to be from 18 to 20 times a minute, and we may add here, incidentally, that during each respiration there are about four heart beats.

Mechanical Work Performed During Respiration.

It will be remembered that in describing the circulation, it was estimated that the mechanical work performed by the heart amounted, in twenty-four hours, to 75,000 kilogrammeters (240 foot tons). We shall see hereafter in the investigation of the source of the energy of the body, that it is equally important to determine, as far as possible, the mechanical work performed by the respiratory muscles. This may be estimated, at least approximately, in the same way as in the case of the heart by multiplying the weight raised by the respiratory muscles by the height. It has already been mentioned that owing to the elasticity of the lungs offering a resistance to the inspired air distending them, the pressure exerted by the latter against the inner surface of the thorax will be less than that exerted by the external air upon the outer surface of the thorax. It is evident, therefore, that at each inspiration, the chest lifts so much of the weight of the external atmosphere as is not neutralized by a corresponding part of the internal one, the weight raised being directly proportional to the elastic tension of the lungs that is to the depth of the inspiration. Let us suppose that the downward pressure of the atmosphere upon the outer surface of the thorax is 15 pounds upon the square inch and the upward pressure of the internal air upon the inner surface 14.8 pounds, or 0.2

[1] Op. cit., p. 88. [2] Op. cit., p. 1085.

pound less, the elastic tension of the lungs amounting to that in easy breathing, and that the chest with an area of 300 square inches is elevated 0.04 of an inch, the work done during each inspiration will be 0.2 foot pounds,[1] and on the supposition that the respirations are on the average 15 per minute, to nearly 2 foot tons[2] per day. The work done by the diaphragm, if calculated in the same way, will amount to about 2.8 foot tons per day; that is if it be supposed that its area is 52 square inches, and that in addition to lifting 0.2 pounds of air through 0.2 in. it overcomes about an equal amount of abdominal pressure. Inasmuch, however, as during inspiration the elasticity of the thoracic walls is overcome by the inspiratory muscles, the work done in this respect would amount, if we assume the former to be equal to that of the elasticity of the lungs to an additional 2 foot tons per day.[3]

Neglecting the weight of the sternum and ribs 14 oz. lifted during sleep or when the body is in the recumbent position, the total work done by the inspiratory muscles would amount to nearly 7 foot tons (2177 kilogrammeters) per day and in deep breathing to more than twice as much. The above estimate of the work done is, of course, only an approximate one to be regarded as what may be done by the inspiratory muscles rather than what is done. Inasmuch as we have seen that expiration in easy breathing is a passive process, a return to the condition of equilibrium, no work is done by the expiratory muscles. If, however, expiration becomes forced, then the work done may amount to nearly as much as that in inspiration.

Breathing Capacity.

On account of the importance of ventilation, of estimating the amount of oxygen absorbed, and carbon dioxide exhaled, of determining the amount of heat produced in the body, etc., it is necessary that the amount of air inspired and expired during respiration should be actually measured. For this purpose we make use of the spirometer. The instrument described by Hutchinson,[4] consists (Fig. 200) essentially of a cylindrical vessel (A), containing water, out of which a receiver (B) can be elevated by breathing into it through a tube (C), the height to which the receiver is elevated and depressed, as shown by the scale D, indicating the volume of the air expired. In using the spirometer, it should be placed upon a firm, level table, about three feet from the ground. The water tap W then having been turned off, and the air tap T opened, clear, cold water is poured through the spout of the cylindrical vessel A, until it is full, any excess of water running off by the tap in communication with the air tube. The counterpoising

[1] $0.2 \times 0.04 \times 300 = 2.4$ inch pounds $= 0.2$ foot pounds $= 0.027$ kilogrammeters.

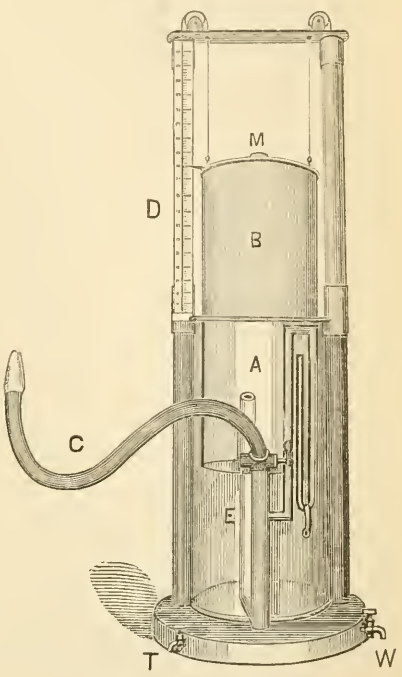
[2] $0.2 \times 15 \times 60 \times 24 = \frac{4320}{2240} = 2$ foot tons $= 871$ kilogrammeters.

[3] It must be admitted, however, that the elasticity of the thoracic walls has not been determined.

[4] Op. cit., p. 1069.

weights being then suspended within the framework M, and over the pulleys, and the air tap closed, the instrument is ready for an observation. The person whose breathing capacity is to be determined standing erect with head thrown backward, and loosely attired, applies by the mouth-piece the flexible tube C to his mouth and expires into the spirometer. The air from his lungs passes thence into the tube E, elevating the receiver B, the volume of air expired, expressed in cubic inches, being shown by the number of the scale to which the index connected with the receiver has been elevated. On the other hand, by inhaling through the tube C, the receiver B will descend, the amount of air inspired being indicated by the scale now read, however, in the reverse direction. The volume of air must, however, be corrected for temperature, for the temperature of the air will be at once reduced to the temperature of the water in the spirometer, to which it has passed, and which is warm or cold according to the season. Practically the change in the bulk of the air will amount to about $\frac{1}{500}$ for every degree Fahr., and the difference should be added or subtracted as the temperature of the room in which is the spirometer is below or above 60°. Suppose, for example, 295 cu. in. be breathed into the spirometer, the temperature of the room being 55°, then 2.9 cu. in. should be added to the 295 cu. in., since $\frac{5}{500}$ equals $\frac{1}{100}$ of 295, equals 2.95 cu. in.; on the other hand, if the air be at a temperature of 70°, then 5.9 cu. in. should be subtracted from the 295, since $\frac{10}{500}$ equals $\frac{1}{50}$ of 295, equals 5.9 cu. in. The U-shaped tube acts as a gauge, since, as long as the colored fluid that is put into it remains at the same level in its two limbs, the density of the air within and without the receiver is the same, which is necessarily an indispensable condition in the working of the instrument. In order to expel the air from the receiver, and return it to its original position, the plug M is removed with one hand, while the receiver is depressed with the other. The experiments having been concluded, and it is desired to empty the water out of the spirometer,

FIG. 200.



Hutchinson's spirometer.

it is only necessary to open the water-tap. If a healthy adult breathe easily into the spirometer in the manner indicated, it will be found that usually about 30 cu. in. (489 c. c.) pass into the instrument with each expiration. If now the air be expelled, and the receiver returned to its original position, and the air-tap be opened, fresh air will pass freely into the receiver, and, the pressure of the air within and without being the same, the receiver will be elevated by the counterpoising weights. Suppose a hundred cubic inches of air have been passed in this way into the receiver, and now a gentle inspiratory effort is made, the receiver will descend, and it will be found that its index has fallen to the number 70 on the scale, showing that 30 cu. in. of air have been inspired. By experimenting in this way upon a number of persons, it will be found that, *cæteris paribus*, on the average, that in easy, tranquil breathing about 30 cu. in. of air are taken into the lungs with each inspiration, and about 30 cu. in. are given out with each expiration. In reality the expired air is about $\frac{1}{50}$ to $\frac{1}{70}$ less in volume than the inspired air. This is due, as we shall see, to the fact of the carbon dioxide excreted being a little less in amount than the oxygen absorbed. The 30 cu. in. of air inspired and expired during each respiration are usually known as the tidal or ordinary breathing air. If now a forcible expiration be made, not only will 30 cu. in. of air pass into the spirometer, as in easy breathing, but as much as 100 additional cu. in. This extra quantity, so to speak, of expired air is not usually changed in respiration, but only when the necessity is felt of more completely renovating the air in the lungs, and is called, therefore, the reserve or supplemental air, and amounts to about 100 cu. in. (1630 c. c.). In prolonged expiratory efforts, such as sneezing and blowing, this reserve air is more or less expelled. As the reserve air is vitiated through continually receiving water and carbon dioxide from the blood of the lungs, pearl-divers and others who are in the habit of temporarily arresting their respiration, instinctively first get rid of their reserve air by forcibly expiring several times, and then fill their lungs with fresh air. If the chest be now enlarged by a forcible inspiration instead of an expiration, the spirometer having been suitably arranged, as much as 110 cu. in. can be withdrawn from the instrument over and above the 30 cu. in. due to an ordinary inspiration. This constitutes what is known as the complemental air, and usually amounts to 100 cu. in. (1630 c. c.). It is drawn upon whenever an effort is made that demands a temporary arrest of respiration, in blowing, yawning, sneezing, etc., to a certain extent in sleep, when the breathing is deep, at the moment immediately preceding some muscular effort, etc. The complemental air can also be indirectly estimated by deducting the sum of the tidal and reserve airs (30 cu. in. plus 100 cu. in.) from the volume of the extreme breathing air, or that which can be expelled from the lungs by the most forcible expiration after the most profound inspiration, and which, we shall

see in a moment, amounts to 230 cu. in.; thus 230 cu. in. less 130 cu. in. equals 100 cu. in. The capacity of the lungs, and the fact that after death they always contain air, make it evident that the air is never entirely expelled, even by the most powerful expiration. A certain quantity of air, therefore, always remains in the lungs. It is known as the residual air, and may be approximately considered as amounting to 1630 c. c. (100 cu. in.). The amount of residual air cannot be determined directly since the volume of air within the lungs after an ordinary expiration consists of the sum of the reserve and residual airs. If this, however, can be determined, the deduction from it of the reserve air will give the residual air. It is well known that hydrogen gas when inspired is not absorbed by the blood, and that gases will diffuse into each other until the mixture becomes uniform. Such being the case, let us suppose that 1000 c. c. of hydrogen be inspired and that 100 c. c. of the mixture is shown by analysis to contain 23.5 parts of hydrogen, the whole mixture will then be 4459 c. c. ($23.5 : 100 :: 1000 : x = 4455$),[1] deducting 1000 c. c. as expired, the remainder 3255 c. c. will be the sum of the reserve and residual volumes from which by subtracting the reserve volume 1630 c. c. we obtain the residual volume 1625 c. c. (99.6 cubic inches).

Assuming the mean capacity of the chest to amount to 312 cu. in., and allowing 100 cu. in. for the heart and great blood vessels, and 100 cu. in. for the parenchymatic structure of the lungs, there would remain little more than 100 cu. in. for the residual air, which is the estimate given by Hutchinson.

While the method just described gives a sufficiently accurate determination of the respiratory capacity, more exact results are obtained when the tube of the spirometer communicates with a mask closely fitting to the face of the person experimented upon. The mask is provided with two openings furnished with valves working in opposite directions. Through one of the openings the expired air is expelled, while through the other the air to be inspired passes from the spirometer. A more simple and equally effective apparatus consists of two ivory tubes which are inserted tightly into the nostrils and which connect with a common tube, dividing into two branches; one of these communicates with the spirometer and transmits the air to be breathed, the other allows the expired air to escape. Each of the branches is provided with a valve which opens in opposite directions. According, therefore, to which of the ivory tubes is inserted into the nose the air can be either inspired from or expired into the spirometer.

We have incidentally alluded, a moment since, to the extreme breathing capacity; by this is meant the volume of air which can be expelled from the lungs by the most forcible expiration, after the most profound inspiration, or the volume that can be inspired by the most forcible inspiration after the most profound expiration.

[1] N. Grehant, Journal de l'Anatomie, 1864, p. 523.

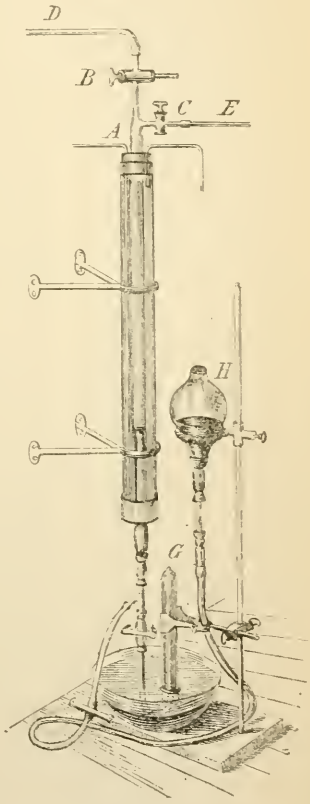
It was called by Hutchinson[1] the vital capacity, as signifying the capacity or volume of air which can only be displaced by living movements, and was determined by this observer to amount in a man of medium height (5 feet 8 inches) to 3749 c. c. (230 cubic inches), being equal to the sum of the tidal reserve and complemental airs.

The experiments upon which this conclusion was based were made by means of the spirometer, upon nearly 5000 persons. Hutchinson also showed that the vital capacity is influenced by various conditions. Thus, it was ascertained that, for every inch of height between five and six feet, the extreme breathing capacity is increased eight cubic inches. The position of the body affects the vital capacity. Thus, in one individual while standing erect, it was 260 cubic inches, and when recumbent it was 230, a difference of 30 cubic inches. The vital capacity is influenced, without doubt, by weight, but, as the weight usually increases with the height, it is difficult to separate the effect of one from that of the other. Age has also an influence, the vital capacity increasing up to the thirtieth year of life, and then diminishing to the sixtieth. The vital capacity is also affected by the sex, being greater, as shown by Herbst,[2] in the male than in the female. As might be anticipated, any diseased condition affecting the mobility of the thorax or the dilatability of the lungs, will modify, more or less profoundly, the extreme breathing capacity, hence the importance of the latter as a test of health or disease. Inasmuch as the extreme breathing air is made up of the tidal reserve and complemental airs, the latter will be affected by the same conditions as the former. As the effects, however, are less marked than where the whole volume of air is considered, it will be necessary to call further attention to them. When it is remembered that, with each inspiration, only about twenty cubic inches of air are introduced, sufficient to fill the trachea and large bronchial tubes, it is evident that there must be some subsidiary force acting in addition to the ordinary respiratory movements of the chest by which the fresh air is brought to the air cells and the vitiated air expelled. The interchange between the fresh air in the upper part of the lungs and the vitiated air in the lower part, is undoubtedly due to the diffusion of the air containing oxygen and carbon dioxide, and which goes on, according to the law established by Graham,[3] that the diffusibility of gases is inversely proportional to the square root of their densities —that is, that the diffusion of oxygen is to the diffusion of carbon dioxide as the square root of the density of carbon dioxide, or $\sqrt{1.529} = 1.237$, is to the square root of the density of oxygen, or $\sqrt{1.1056} = 1.0514$, or $1.237 : 1.0514 :: 95 : 81$. According to this law, then, the lighter gas, the air, with its oxygen, will descend more rapidly than the carbon dioxide, the heavier gas, will

[1] Op. cit., p. 1067. [2] Meckel's Archiv f. Anat. u. Phys., p. 3, s. 103, 1828.
[3] Trans. of Royal Soc. Edinb., Vol. xii., p. 573, 1834.

ascend, 91 parts of oxygen replacing 81 parts of carbon dioxide. As this diffusion is continually going on between these gases, the air in the pulmonary air cells, where the exchange between the oxygen and carbon dioxide takes place, has a tolerably uniform composition, and the aëration of the blood is far less intermittent in its character than the respiratory movements of the thorax. The passage of the oxygen from the air of the pulmonary air cells into the blood of the pulmonary capillaries, and of carbon dioxide in the reverse direction from the blood into the air, is due to the fact of the tension of the oxygen of the air being higher than that of the blood, and of the tension of the carbon dioxide of the blood being higher than that of the air. Necessarily, therefore, the oxygen of the air within the lungs will pass through the wall of the air cell and capillary into the blood, thence into the red corpuscles, combining, as we have seen, with the hæmoglobin of these bodies, while the carbon dioxide will pass in the reverse direction from the blood through the wall of the capillary and wall of the air cell into the lungs, and thence out of the body. It is possible that the pulmonary epithelium in acting as a secretory surface may also exercise some influence in promoting the absorption of oxygen and elimination of carbon dioxide. On the other hand, the oxygen of the arterial blood leaving the hæmoglobin will readily diffuse through the capillary into the tissues, the tension of the oxygen in the latter being so low as to amount, practically, to nothing, the oxygen combining in some stable form as rapidly as absorbed. While, owing to the continual production of carbon dioxide in some unknown way in the tissues out of the oxygen absorbed, the tension of the carbon dioxide of the tissues being always higher than that of the blood circulating in their midst, the carbon dioxide will consequently diffuse in the opposite direction to that of the oxygen, viz., from the tissues through the wall of the capillary into the blood now become venous through deoxidation of most of its hæmoglobin. The tension of the gases in the blood is determined by means of the ærotonometer. This (Fig. 201) consists of a long glass tube *A*, communicating above by means of the stopcocks *B C*

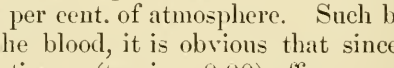
FIG. 201.



Ærotonometer.

with a tube (*D*), bringing the blood, the tension of whose gases is to be determined, and with one (*E*) leading to the eudiometer for the determination of the gases, and below with a bell-jar (*G*), standing over mercury and with the reservoir of mercury *H*. The glass tube is first entirely filled with mercury so as to exclude the air, by elevating the reservoir *H*, and is then surrounded by hot water so as to maintain the temperature of the blood examined at that of the animal from which it was drawn. The glass tube *A* is then filled through the depression of the mercurial reservoir with a mixture consisting of known quantities of nitrogen, oxygen, and carbon dioxide. The blood being allowed to flow from the artery or vein of the animal for a moment out of the tube *D*, so as to exclude the air, is then diverted into the gas mixture in *A*. As the blood flows down through the tube into the mercury, the latter is driven up into the bell-jar *G*, while the tension of its oxygen and carbon dioxide are increased or diminished according to the corresponding tension of the oxygen and carbon dioxide of the gas mixture, as finally determined by the analysis of the gases in the eudiometer *E*, into which the gases are driven by the elevation of the mercurial reservoir. The general results as to the tension of the oxygen and carbon dioxide in the blood as obtained with the ærotonometer by Pflüger,[1] Wolfberg,[2] Strassburg,[3] Nussbaum,[4] are as follows: The tension of oxygen in arterial blood (one atmosphere = 760 mm. of mercury) is equal to 29.6 mm. of mercury, corresponding to 3.9 per cent. of atmosphere (760 : 29.6 :: 100 : $x = 3.9$), that of carbon dioxide being equal to 21.2 mm., corresponding in amount to 2.8 per cent. of atmosphere. The tension of oxygen in venous blood is 22.04 mm. of mercury, corresponding to 2.9 per cent. of atmosphere, that of carbon dioxide being equal to 41 mm. or 5.4 per cent. of atmosphere. Such being the tension of the gases of the blood, it is obvious that since the tension of the oxygen in the tissues (tension, 0.00) offers no resistance to that of the oxygen of the arterial blood (tension, 29.6) and as the tension of the carbon dioxide of the arterial blood (tension, 21.2) is less than that of the tissues (tension, 58, possibly), that the oxygen of the arterial blood will pass through the wall of the capillary into the tissues and the carbon dioxide formed in the latter into the blood as follows:

Relative Tension of Oxygen and Carbon Dioxide in Arterial Blood and Tissues.

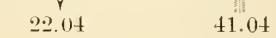
	Oxygen.	Carbon dioxide.
Tension in arterial blood	29.6 mm. Hg	21.2
Wall of capillary		
Tension in tissues	0.0	58.2

On the other hand, it has been shown, by catheterizing the lungs,[5] that although the tension of the carbon dioxide of the at-

[1] Pflüger's Archiv, Bd. vi., s. 43. [2] Ibid., Band iv., s. 465.
[3] Ibid., Band vi., s. 65. [4] Ibid., Band vii., s. 296. [5] Pflüger's Archiv, loc. cit.

mosphere amounts to only 0.30 mm. of mercury (0.04 per cent. of an atmosphere), that of the air of the alveoli, or cells, may be as much as 29.1 mm. (3.84 per cent. of an atmosphere), and that while the tension of the oxygen of the atmosphere is 158.15 mm. (20.8 per cent. of an atmosphere), that of the alveolar air may be reduced to 138 mm. (18.2 per cent. of an atmosphere). If it be admitted that the relative tensions of the gases are such, then the tension of the carbon dioxide of the venous blood (tension 41) being greater than that of the alveolar air (tension 29.1) and the tension of the oxygen of the alveolar air (tension 138) being greater than that of the venous blood (tension 22), the carbon dioxide of the venous blood will pass through the wall of the lung into the alveolar air, and the oxygen of the latter into the venous blood, as follows:

RELATIVE TENSION OF OXYGEN AND CARBON DIOXIDE IN ATMOSPHERE, AIR OF ALVEOLI AND VENOUS BLOOD OF LUNGS.

	Oxygen.	Carbon dioxide.
Tension in atmosphere . .	158.15 mm.	0.30
Tension in air of alveoli . .	138.00	29.10
Wall of lung		
Tension in venous blood . .	22.04	41.04

The amount of the gases and the condition in which they exist in the blood have already been considered.

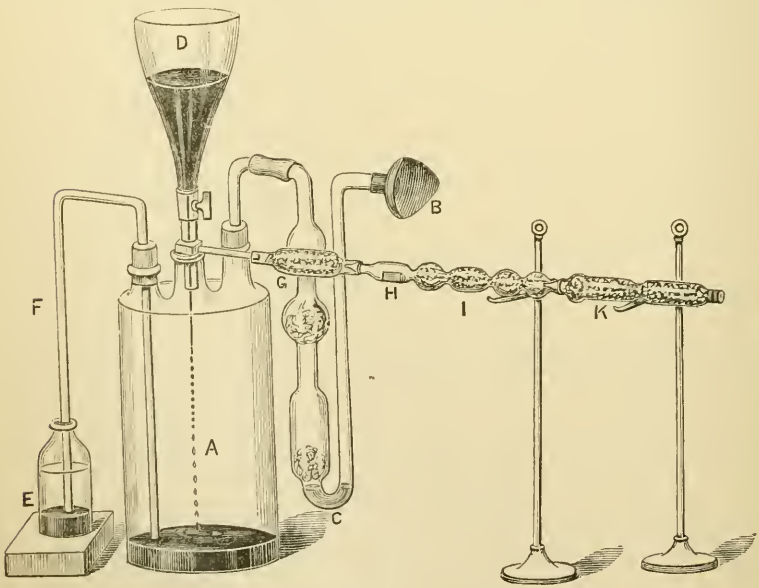
CHAPTER XXIII.

RESPIRATION.—(*Continued.*)

ABSORPTION OF OXYGEN.—EXHALATION OF CARBON DIOXIDE.

Having seen that the essence of respiration consists in the absorption of oxygen, and giving up of carbon dioxide, and the manner in which the air containing these gases is respired, it remains for us now to determine as far as possible the amount of oxygen absorbed and carbon dioxide exhaled in a given time. This is one of the most important problems in experimental physiology, since, as we shall see, the amount of heat and energy liberated in the body will depend upon the amount of oxygen absorbed, and carbon dioxide and water exhaled. The amount of oxygen absorbed from, and carbon dioxide exhaled into, a given quantity of air can be determined among other means by the Valentin and Brunner apparatus.

Fig. 202.

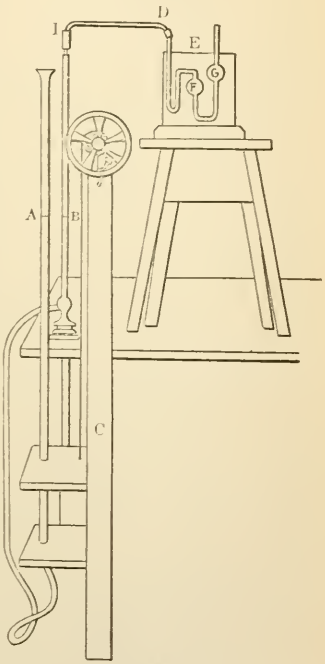


Valentin and Brunner's respiration apparatus.

This consists (Fig. 202) of a Woulff's bottle A having a capacity of nearly a liter (61 cu. in.). One of the openings communicates with the mouth-piece B, into which the person expires, the air first passing through pumice-stone and sulphuric acid C so as to dry it.

The middle opening communicates with the set of tubes G H I K. H and I contain phosphorus and baryta for the absorption of the oxygen and carbon dioxide of the expired air, G and K pumice-stone, etc., that of G for the absorption of the watery vapors that may have escaped, the pumice-stone, etc., in C K for retaining that taken up by the dry air passing through the baryta solution, and which, if lost, would cause an error in the estimate of the carbon dioxide exhaled, the tubes being weighed before and after the experiment. Through the middle opening of the Woulff's bottle a funnel (D) provided with a stopcock is introduced, the opening being then hermetically closed. The funnel is filled with a known quantity of mercury. The manner of using the apparatus is as follows: having breathed for say fifteen minutes through the mouth-piece until the air of the Woulff's bottle has been entirely displaced by the expired air, the mouth-piece is entirely closed, any external air being further prevented from passing into the Woulff's bottle by the mercury in E acting as a valve, the air-tightness of the apparatus being assured by the rise of the mercury in the tube F, through the contraction of the expired air in A, consequent upon its cooling and the closure of the tube funnel. The stopcock of the funnel being then turned, the mercury passes into the Woulff's bottle, displacing a known quantity of expired air, the latter passing into the set of tubes G H I K, previously adjusted to the middle opening. The weight of the tubes H and I having been previously determined, their increase in weight will give, respectively, the amount of oxygen and carbon dioxide absorbed. Deducting now the amount of oxygen so obtained from the expired air from that contained in an equal quantity of ordinary inspired air, the remainder will be the amount of oxygen retained in the inspiration of such a quantity of air; on the other hand, deducting the trace of carbon dioxide usually present in the atmosphere from that obtained from the expired air, and the remainder will be the amount of carbon dioxide exhaled into such a quantity of expired air.

FIG. 203.



Hempel apparatus.

A much more expeditious method of analysis, however, is that of Hempel.[1] This consists in passing expired air into a gradu-

[1] Neue Methoden für Analyse der Gase, von Dr. W. Hempel, Braunschweig, 1880.

ated burette (Fig. 203 B) filled with mercury, the latter flowing out of the burette as the mercurial reservoir A with which the burette communicates is lowered by means of the wheel work C attached to the solid wooden frame fastened to the table. The sample of gas so obtained reduced to standard temperature and pressure is then driven out of the burette B by elevating the mercurial reservoir into a Hempel pipette F containing a concentrated solution of soda and after remaining there long enough for the absorption of any carbon dioxide present is driven back into the graduated burette by lowering the mercurial reservoir, the diminution in volume, the latter reduced to standard temperature and pressure, representing the carbon dioxide absorbed. The pipette for the absorption of the carbon dioxide being removed, the burette is connected with one containing pyrogallic acid into which the sample of gas just freed of its carbon dioxide is driven by elevating the reservoir and in which it is allowed to remain until the oxygen present is absorbed. The sample of gas being then driven back into the graduated burette by lowering the reservoir the diminution in volume, reduced to standard temperature and pressure, represents the volume of oxygen absorbed.

The ordinary atmospheric air consists in 100 parts of a mechanical mixture rather than a chemical combination, of oxygen 20.81, nitrogen 79.15,[1] and carbon dioxide 0.04 parts. If, however, 100 volumes of expired air be analyzed by either of the two methods just mentioned it will be found that it consists of a mixture of oxygen 16.033, nitrogen 79.587, carbon dioxide 4.38 parts. It will be observed, therefore, that the air in being inspired loses about 4.77 parts oxygen and gains about 4.34 parts of carbon dioxide, the nitrogen remaining practically unchanged in amount. In other words, of a given volume of air breathed about 5 per cent., or $\frac{1}{20}$, will represent the oxygen absorbed and nearly the amount of carbon dioxide expired, the oxygen absorbed not being exactly replaced by the carbon dioxide expired, since, as we shall see presently of the oxygen absorbed, part only is expired as carbon dioxide. Let us turn now to the consideration of the amount of the oxygen absorbed and carbon dioxide expired in twenty-four hours and the conditions influencing the same. If it be admitted that during easy breathing about 500 c. c. (30 cubic inches) of air is inspired and expired at each respiration, and that the number of respirations throughout the day are, on the average, 15 per minute, the air breathed in 24 hours will be 10,800 liters (381 cubic feet) and the oxygen absorbed will amount to 515.16 liters (18 cubic feet), or 738 grammes, and the carbon dioxide to 468.72 liters (16.6 cubic feet), or 926 grammes, as shown in the following:

[1] Including argon, 2 per cent.

AIR INSPIRED IN 24 HOURS, ETC.

500 c. c. of air inspired at each respiration.
15 respirations per minute.
7.5 liters per minute.
60
450 " " hour.
24
10,800 " " day.

$$10{,}800 : 100 :: x : 4.77$$

$x = 515.16$ liters of oxygen absorbed.
1 liter of oxygen weighs at standard pressure and temperature 1.4298 grammes.
515.16 liters weigh 738 grammes.

$$10{,}800 : 100 :: x : 4.34$$

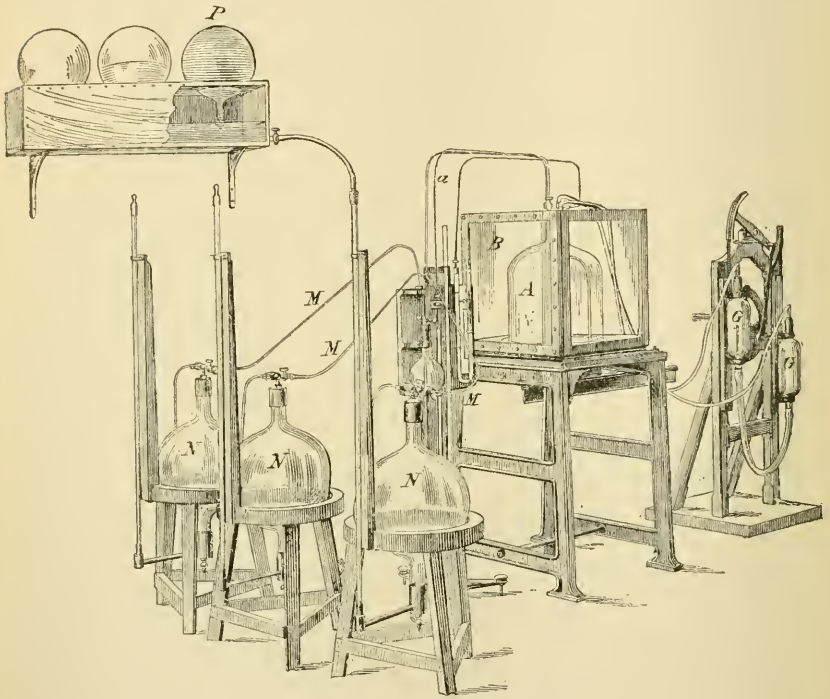
$x = 468.72$ liters of carbon dioxide expired.
1 liter of carbon dioxide weighs 1.966 grammes.
468.72 liters weigh 926 grammes.

It might naturally be asked, even if oxygen is absorbed and carbon dioxide expired in the amounts just stated for a short period of time, does it follow that the total amount of the gases interchanged in the twenty-four hours will be the same as that obtained by the method just given? That such is the case, however, has been proved by experiments like those of Pettenkofer,[1] made with the celebrated respiration apparatus in Munich, large enough to hold a man, and in which the observations extended over a period of twenty-four hours. As might be expected from the nature of the case, the determination of the amount of oxygen absorbed and carbon dioxide expired by a human being in a given time must be of an approximate character. With animals, however, it is different, and especially in the case of small ones, in which the conditions are very favorable, the determination of the oxygen absorbed, as well as the carbon dioxide expired, can be most accurately determined. The most perfect form of apparatus as yet devised for this purpose is that of Regnault and Reiset.[2] It consists essentially of a receiver filled with air enclosing the animal to be experimented upon, and which communicates on the one hand with a reservoir supplying oxygen as fast as it is consumed during respiration, and on the other with an apparatus for the absorption of the carbon dioxide exhaled. The detailed disposition of the apparatus will be understood from Fig. 204. Within the tubulated bell-jar *A*, immersed in the cylinder of water *B*, is placed a little animal, a dog, for example, the subject of the experiment. The animal having been introduced from below, and the opening hermetically closed, the large pipettes *G G*, filled with a solution of potash or soda of known strength and quantity, and communicating with each other by a caoutchouc tube, absorb the CO_2 exhaled into the air of the jar *A*, the air being drawn alternately into the pipettes *G G* through their elevation and depres-

[1] Pettenkofer, Ann. Chem. Pharm. Suppl., B. ii., 1862, s. 1.
[2] Annales de Chimie et de Physique, 3me ser., Tome xxvi., 1849, p. 441.

sion by some mechanical arrangement. According as oxygen is absorbed by the animal, the gas pressure falls in *A*, and consequently the oxygen of the balloon *N*, under the pressure of the calcium chloride solution in *P*, flows through *M*, replacing that lost in *A*. The object of the gas pipette *a* is to enable the observer to draw a small sample of gas out of the chamber for analysis. The temperature and pressure of the gas within the chamber, and the amount of oxygen in the chamber at the beginning and the end of the experiment, as well as that delivered to the chamber being known,

Fig. 204.



Regnault and Reiset respiration apparatus.

the amount of oxygen absorbed by the animal can be determined, the carbon dioxide expired being equal to the difference in the weight of the soda pipettes before and after the experiment.[1] The advantage of this apparatus is that the animal suffers no inconvenience from even a prolonged confinement within the chamber, and that the oxygen is furnished as needed, and the carbon dioxide removed as rapidly as produced. The amount of oxygen absorbed and carbon dioxide expired, etc., by a small monkey during a period of five hours, as determined by means of the Regnault and Reiset apparatus, is given in the accompanying Table :

[1] For a detailed description of the apparatus and the results obtained by it the reader is referred to Researches upon Respiration, by H. C. Chapman and A. P. Brubaker, Proc. Acad. Nat. Sciences, 1891, p. 13.

OXYGEN ABSORBED AND CARBON DIOXIDE EXHALED, ETC., BY A MONKEY (CEBUS CAPUCINUS).[1]

	Grammes.
Weight of oxygen consumed	13.47
Weight of carbon dioxide produced	16.389
Weight of oxygen contained in the carbon dioxide.	11.919
Ratio between the weight of the oxygen contained in the carbon dioxide produced, and the weight of the oxygen consumed	0.884
Weight of oxygen consumed per hour	2.694
Weight of oxygen consumed per hour per kilogramme of animal	1.347
Weight of carbon dioxide produced per hour	3.277
Weight of carbon dioxide produced per hour per kilogramme of animal	1.638

The determination of the amount of carbon dioxide expired in a given time is as important as that of the oxygen absorbed since the carbon dioxide containing part of the oxygen absorbed by the system during some previous period affords the means, therefore, of indirectly estimating the same. In making use of the indirect method of determining the amount of oxygen absorbed by an animal the water exhaled is usually estimated simultaneously with that of the carbon dioxide expired. One of the most accurate forms of apparatus for this purpose is that devised by Voit[2] and which is a modified form of the large respiration apparatus of Pettenkofer already referred to. The small respiration apparatus of Voit (Fig. 205) consists of a chamber H in which the subject of the experiment, a large dog, for example, is placed ;[3] of a large drum, and pumps worked by a water-wheel for the production of a constant draught of fresh air through the apparatus ; of bottles and tubes containing appropriate materials for the absorption of the water and carbon dioxide of the air surrounding the chamber, as well as that from within it ; and of meters for registering the total amount of air that has passed through the chamber, of the fractional part of the same analyzed, and of the air surrounding the chamber analyzed for comparison.

The chamber H in which the animal is placed consists of a zinc framework in which solid glass plates are imbedded, a part of which at the front of the chamber is movable and acts as a door. The other two openings present, are for the entrance and exit of the air ventilating the chamber. The air entering by the opening a, seen through the large chamber M, passes by the pipe to the bottom of the chamber, and having traversed the latter, leaves it at its upper portion by the pipe b and passes thence by the pipe d (disconnected with H in Fig. 205) into the large gas meter 13 (Fig. 206), whence having been measured, it is expelled. The constant current of air so passing is drawn out of the tubes d b and chamber H by the

[1] Chapman and Brubaker, op. cit., p. 44.

[2] Zeitschrift für Biologie, 1875, s. 532.

[3] In that case the tube (Fig. 205) is connected with the tube b of the small chamber H; when the subject of the experiment is a man, however, it is then connected with the tube b of the larger chamber M.

rotation of the drum of the gas meter B, whose axis is in connection with that of the overshot water-wheel G, through the teeth of the cog-wheel on the axis of the gas meter interlocking with those of the cog-wheel on the axis of the water-wheel. The water-wheel

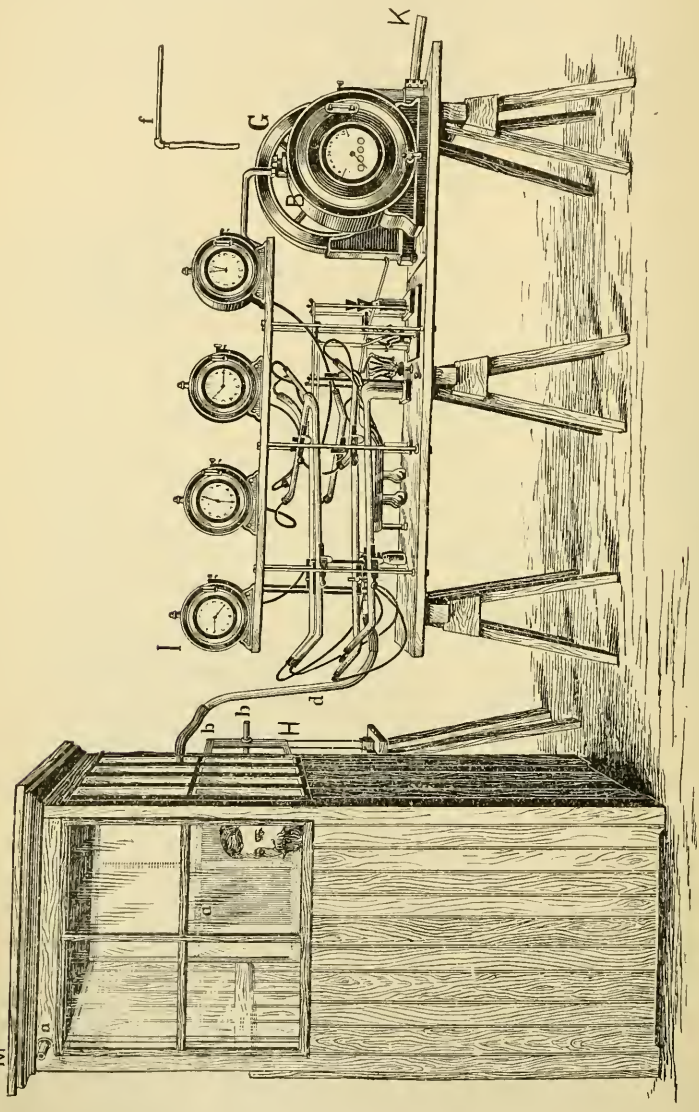


Fig. 205. Volt's respiration apparatus with additional chamber for man.

is kept uniformly rotating through the flow of water from the pipe f connected with a small reservoir, the latter communicating in turn with that supplying the building, the water emptied by the buckets of the water-wheel passing into a trough is carried away by the waste pipe K. Inasmuch however, as with the water-wheel

rotating only once a minute and the experiment lasting but six hours over 10,000 liters of air pass through the chamber it is obvious that the analysis of such a large volume of air would involve a great expenditure of time and labor. This is avoided by diverting part of the air, which issues from the chamber, by means

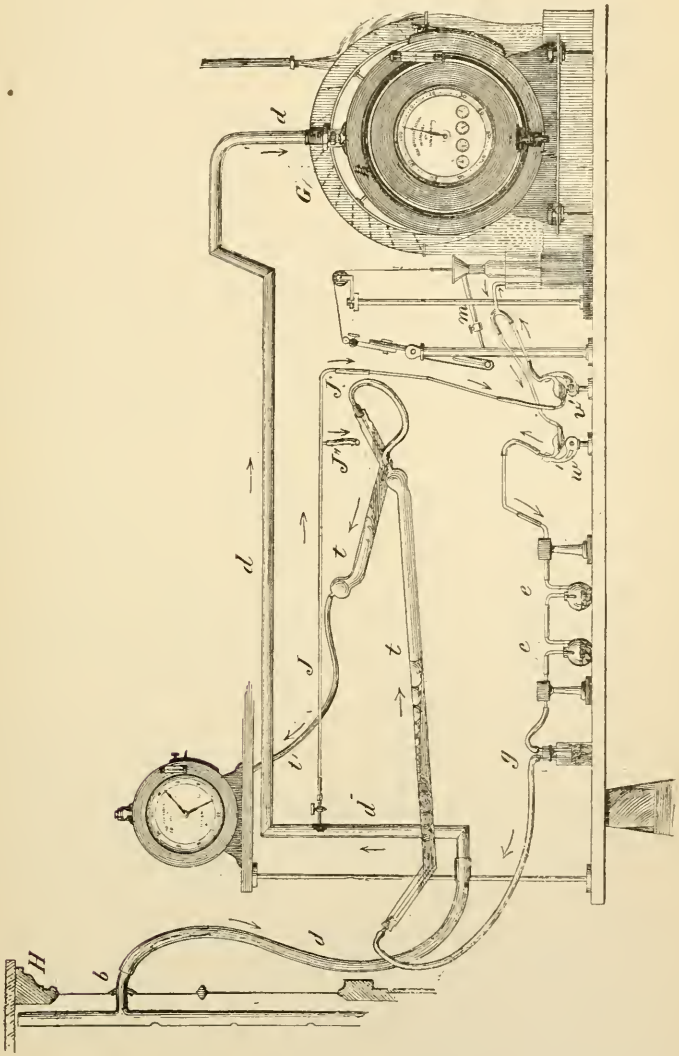


FIG. 206.

Illustrating the connection of the tubes with one meter only, lettering same as in Fig. 205.

of mercurial pumps, from the tube d into the tube J, terminating in the two branches J'' and J' and of determining the amount of carbon dioxide and water in two samples of air. The air from J' passes through the valve v' as the pump is elevated by the crank connected with the axis of the water-wheel and returns through the valve w' as the pump is depressed, thence into the short bottles

e e containing pumice-stone and sulphuric acid for the absorption of the water, and through the large bottles *g* containing water and pumice-stone for resaturation, then through the tubes *t t*, containing a solution of baryta, for the absorption of the carbon dioxide, finally escaping by the meter, where it is measured. The air in *J''* after having passed through a similar set of valves, tubes, etc., escapes by a second meter where it is measured. By this arrangement, two samples of air are therefore analyzed, the mean of which represents the amount of carbon dioxide and water in a given volume of air.

As the external air passing into the chamber contains carbon dioxide and water as well as the internal air, the amount of the same must be determined. This is done in exactly the same way as in the case of the internal air, the external air being drawn into a tube by two pumps and passed through a double set of bottles, tubes, and meters similar to those described. The amounts of carbon dioxide and water in a given volume of air surrounding the chamber, having been determined, this is deducted from the carbon dioxide and water in an equal volume of air that has passed simultaneously through the chamber, the difference giving the amount of carbon dioxide and water expired by the animal into a given volume of air.

It remains for us now to describe a little more in detail than we have done the manner in which the water and carbon dioxide are determined by means of the absorbing apparatus. The determination of the amount of water is very simple. The bottles (*e, e*, Fig. 206) through which the air from within and without the chamber passes contain, as already stated, pumice-stone and sulphuric acid, which has a great avidity for water. These being weighed in scales, before and after the experiment, the difference will give the amount of water in the air from within and without the chamber; the latter amount, as we have already mentioned, must be then deducted from the former, in order to get the amount of water exhaled by the animal. Water having been absorbed as the air passes through the bottles the dried air is resaturated as it passes the bottles *g*, the saturated pumice-stone within them giving up the water it contains. Were not the air so resaturated it would take up water from the solution of baryta through which the air next passes, and this must be avoided, as the solution of baryta is used for the absorption of carbon dioxide.

The amount of carbon dioxide absorbed is determined by neutralizing the baryta solution by oxalic acid before and after the experiment, the browning of turmeric paper being used as an indication of the point of neutralization. The method will be made clear by the following example. Suppose, before an experiment with the respiration apparatus, it was ascertained by the means just described that exactly 72.4 c. cm. of oxalic acid neutralized 25 c. cm. of the standard baryta solution, it will be found that at the end of the experiment it requires only 61.8 c. cm. of oxalic acid, or 10.6 c. cm.

less, to neutralize 25 c. cm. of the baryta solution, drawn out of the tubes by means of a pipette. As the carbon dioxide passes through the latter during the experiment it combines with part of the baryta, and there is, therefore, less baryta to combine with the oxalic acid after the experiment than there was before. Now, as for each milligramme of carbon dioxide that combines with the baryta during the experiment there will be 1 c. cm. less of oxalic acid required for neutralization after experiment, it follows that 10.6 milligrammes of carbon dioxide must have been absorbed by the 25 c. cm. of the baryta solution, since it requires 10.6 c. cm. less of oxalic acid for neutralization after the experiment than before. In other words, the baryta before the experiment combined with 72.4 c. cm. of oxalic acid, after the experiment with 61.8 c. cm., because during the experiment it combined with 10.6 milligrammes of carbon dioxide, which are volumetrically equal to 10.6 c. cm. of oxalic acid. Let us suppose, for example, that by the method just described the amount of carbon dioxide and water expired by an animal into a given volume of air has been determined, then the total amount of carbon dioxide and water expired by the animal at the end of the experiment would be obtained by multiplying the amount of carbon dioxide and water in the given volume of air by the ratio of the latter to the volume of air that has passed through the large and the two small meters (internal air) and that still remains in the chamber *II* and the tube *b d J*, and adding up the respective quotients.

RESULTS OF EXPERIMENT UPON A CAT, OBTAINED WITH THE VOIT RESPIRATION APPARATUS. DURATION OF EXPERIMENT, SIX HOURS.

Calculation for Carbon Dioxide and Water.

	Carbon dioxide.	Water.
In 1000 liters of inner air . .	1.8085 grammes.	12.457 grammes.
In 1000 liters of outer air . .	0.5815 "	11.445 "
Difference	1.2270 "	1.012 "
In 11600.5 liters of large meter .	14.23 "	11.74 "
In 66.55 liters chamber and tube .	0.11 "	0.07 "
In 121.02 3d and 4th meters . .	0.15 "	0.12 "
Total	14.46 "	11.93 "

Calculation for Oxygen Absorbed.

Before experiment.		After experiment.	
Weight of animal	3001.3 grms.	Weight of animal . .	2987.80 grms.
Ingesta . .	0.0 "	Egesta urine . .	0.0 "
		Egesta feces . .	0.0 "
		Egesta water . .	11.93 "
		Egesta carbon dioxide	14.46 "
Total .	3001.3 "	Total . . .	3014.19 "
			3001.30 "
The quantity of oxygen absorbed equals the difference, viz.:			12.89 "

$$\frac{\text{Weight of oxygen in carbon dioxide expired}}{\text{Weight of oxygen absorbed}} = \frac{10.51}{12.89} = 0.81$$

By substituting for the chamber (*H*) containing the animal one large enough to hold a human being (Fig. 211, *M*) the carbon dioxide expired by a man in twenty-four hours has been found to amount, upon a mixed diet, to 930 grammes (32.08 ounces), and which contains 253.6 grammes (8.9 ounces) of carbon. The water exhaled by a man in the same period of time cannot, however, be accurately determined by this apparatus, so much of it being precipitated in the chamber, and is estimated, as we shall see presently, by another method. The estimate of the amount of carbon dioxide expired by a man in twenty-four hours just given does not differ essentially from that of Andral and Gavarret[1] (921 grammes), though greater than that of Edward Smith[2] (760 grammes). The experiments of these observers were made with the object of determining only the carbon dioxide exhaled, and the apparatus consisted in both instances of a mask closely fitting the face, having two openings provided with valves for the entrance and exit of the air, the carbon dioxide exhaled in the experiments of Andral and Gavarret being determined by means of a solution of potash contained in U tubes, and in those of Smith by a solution of potash arranged in numerous layers. The mechanical details of the apparatus made use of by these observers, as well as by their predecessors, Lavoisier and Seguin, Prout, Davy, Dumas, Allen and Pepys, Scharling, and others, not being as perfect as those of the Pettenkofer-Voit respiration apparatus, just described, it would be superfluous to dwell further upon them. In this connection, however, it is proper that some allusion at least be made to the indirect method of determining the amount of carbon dioxide exhaled in a given time, so successfully applied in the case of large animals by Boussingault.[3] This method consists of so regulating the diet of the animal experimented upon, a horse or cow, for example, that there is no loss of weight during the experiment, and of weighing everything introduced as food, solid and liquid, and all discharged as urine or feces. Knowing the quantity of carbon entering the body in the food, and leaving it in the urine and feces, the difference between the carbon of the latter and the former (that of the food being in excess) will be the amount of carbon leaving the body by the lungs and skin. As regards the carbon excreted by the skin, it can, for such approximate determinations, be neglected, since, as we shall see, when the skin is considered as a respiratory surface, the carbon dioxide exhaled does not amount to more than between $\frac{1}{50}$ and $\frac{1}{200}$ of the total amount excreted.

The amounts of oxygen absorbed and carbon dioxide expired in twenty-four hours, while on the average about what we have stated, are, nevertheless, affected by numerous conditions. Among the most important of these are the rapidity of the respiratory move-

[1] Ann. de Chimie et de Physique, 3me serie, Tome viii., p. 129.
[2] Phil. Trans., Vol. 149, 1860, p. 681.
[3] Mem. de Chimie agricole et de Physiologie, pp. 1–12. Paris, 1854.

ments, sex, age, food, digestion, exercise, fatigue, sleep, season, temperature, period of the day, moisture, atmospheric pressure, nervous system, species, body weight and body surface of animal. Let us consider the influences exerted by the above somewhat in detail. The osmosis of the oxygen of the air and the carbon dioxide of the blood within the pulmonary capillaries not being a sudden action, but a continuous one, the amount of the gases so interchanged will naturally depend on the length of time during which the air remains in contact with the respiratory surface; thus, Vierordt,[1] in the experiments performed upon his own person, found that, when he breathed as slowly as possible, 6 per cent. of CO_2 was exhaled in each expiration, but that when he breathed as rapidly as possible only 3 per cent. as shown in the following Table:

Per cent. of CO_2 in expired air.	No. of expirations per minute.
5.9	6
4.3	12
3.5	24
3.1	48
2.9	96
2.8	150

It does not follow, however, that because the per cent. of carbon dioxide contained in each expiration is greater during slow than in rapid breathing that more carbon dioxide is expired in a given period in the former case than the latter. On the contrary, the reverse obtains, since the small per cent. of carbon dioxide that each expiration contains during rapid breathing is more than compensated for by the greater number of expirations. Thus, suppose, for example, that 250 c. cm. of air are expired six times in a minute, then, as each 100 c. cm. contain 5.9 c. cm. of carbon dioxide: $5.9 \times 2.5 \times 6$, or 88.50 c. cm., will be the amount of carbon dioxide expired in the given time. On the other hand, if the same quantity of air be expired twelve times in a minute, each expiration will contain only 4.3 per cent. of carbon dioxide, and yet 129 c. cm. of carbon dioxide will be expired in the given time, since $4.3 \times 2.5 \times 12$ equals 129. According to the same authority if an expiration be divided into two equal parts, the first part will contain, on an average, 3.72 per cent. of carbon dioxide, the second 5.44 per cent., the air exhaled during the first period of the expiration containing less carbon dioxide than that exhaled during the second period. The amount of carbon dioxide exhaled by an individual depends also upon the sex. Thus, it has been shown by Andral and Gavarret[2] that one more gramme of carbon (corresponding to 1.85 liters of carbon dioxide) was exhaled per hour by the male than by the female. Indeed, the difference amounted in some instances to even as much as 7 liters. The difference in the weight

[1] Physiologie des Athmens, p. 102. Karlsruhe, 1845.
[2] Op. cit.

of the body was not taken into consideration in the observations of Andral and Gavarret. Scharling,[1] however, found that more carbon dioxide was exhaled by the male than the female, even when this was estimated with reference to the body weight. Apart from the greater muscular activity of the male, as compared with the female, being sufficient to account for the difference in the amount of carbon dioxide exhaled by the sexes, other conditions peculiar to the female exert an influence in this respect that must not be overlooked. Thus it was shown by the experiments of Andral and Gavarret,[2] that as long as the menses succeeded each other regularly, the average amount of carbon dioxide exhaled remained about the same, being on the average 11.7 liters per hour, with their cessation the amount increased to about 15 liters, while from 60 to 82 years of age it diminished from 13 to 11 liters. Temporary cessation of the menses whether due to pregnancy or other causes, is also accompanied by an increase of the amount of carbon dioxide exhaled.

As is well known, during the first few hours and days after birth, the infant making little or no movement, sleeping most of the time, generates but little heat, and must, therefore, be carefully guarded against changes in the external temperature. At this early period of life the amount of oxygen absorbed and carbon dioxide exhaled must be very small. With the thorough establishment of respiration, this amount is increased, and from the fact of the number of respirations being greater in early than in later life, it is probable that the amount of carbon dioxide exhaled, considered with reference to the body weight is greater in the infant than in the adult. The necessary data essential for such a comparison are, however, too insufficient to admit of more than the general statement just made. From the observations of Andral and Gavarret[3] based upon the examination of numerous individuals between the ages of 12 and 102 years, we learn that from the age of 12 to 32, there is an absolute increase in the amount of carbon dioxide exhaled, from 32 to 60 years old a slight diminution, and from 60 to 102 years, a very considerable one.

Males.	Carbon dioxide exhaled per hour.
12 to 16 years of age.	15 liters (915 cubic inches).
17 " 19 " "	20 "
25 " 32 " "	22 "
32 " 60 " "	20 "
63 " 82 " "	15.3 "
102 " "	11 "

When these observations are supplemented by those of Scharling,[4] we also learn that the amount of carbon dioxide exhaled in youth, relative to the weight of the body, is greater than that in the adult, being in the case of a boy, for example, twice as much

[1] Ann. de Chimie, Tome viii., 1843, p. 486.
[2] Op. cit.
[3] Op. cit.
[4] Op. cit., p. 129.

as in a man. The results of Scharling's experiments might be inferred from those of Andral and Gavarret, since the absolute increase in the amount of carbon dioxide exhaled between the period of childhood and adult life is small, as compared with the increase in the weight of the body within the same period.

According to Pettenkofer,[1] more oxygen is absorbed upon a nitrogenous than upon a non-nitrogenous diet, and more upon a non-nitrogenous one than upon a mixed one, the interchange of oxygen and carbon dioxide being, as might be expected, least during fasting, as was shown by the following results obtained by the above observers.

	Fasting.	Mixed diet.	Non-nitrogenous diet.	Nitrogenous diet.
Oxygen .	743 grms.	709 grms.	808 grms.	850 grms.
Carbon dioxide	695 "	912 "	839 "	1003 "

It will be observed that it is only in the case where no food was taken that the oxygen absorbed is greater than that of the carbon dioxide expired.

As regards the influence of the food upon the exhalation of carbon dioxide, the extended series of experiments performed by Dr. Edward Smith[2] upon himself and friends, are very conclusive. Food, with reference to the exhalation of carbon dioxide, can be divided, according to Dr. Smith, into two classes, respiratory excitants, which increase the exhalation of carbon dioxide, and non-exciters, which diminish it. The excito-respiratory foods include the nitrogenous articles of diet, milk, sugar, rum, beer, stout, the cereals, and potato; the non-exciters, starch, fat, certain alcoholic compounds, the volatile element of wines and spirits, and coffee leaves. The most powerful respiratory excitants are tea and sugar, coffee, rum, milk, cocoa, ales, and chicory come next, then casein and gluten, and lastly gelatin and albumin. The effect of taking respiratory excitants is soon experienced by the system, the maximum effect being usually attained within an hour; their action is of a temporary character, and the effect is not proportional to the quantity taken. Certain respiratory excitants, like tea and coffee, cause an exhalation of carbon in excess of that supplied by these foods, while others, like sugar, cause an evolution less in amount than that supplied. In this connection it may be mentioned that the soothing influence experienced by persons suffering from depression of spirits by drinking tea is probably due to the exhalation of carbon dioxide being increased, an excess of carbon dioxide in the system giving rise to such feelings. According to Dr. Smith, brandy, whiskey, and gin, the volatile elements of alcohol, gin, rum, sherry, and port wine, when inhaled diminished the quantity of carbon dioxide inhaled, while rum and malt liquors, on the con-

[1] Sitzungber. d. Konigl. bayer Acad. d. Wissen., 1867, s. 255.
[2] Ph. Trans., Vol. 149, 1860, p. 715.

trary, increased the exhalation. While the effect of pure alcohol, according to Prout, Horn, and Vierordt,[1] is to diminish the exhalation of carbon dioxide, just the opposite effect is attributed to it by Hervier and St. Leger and Smith. The difference in the result of the effect of alcohol upon the exhalation of carbon dioxide observed by these experimenters may be due to the proportion of carbon dioxide in the expired air being only considered, and not the absolute quantity exhaled, as was the case in the experiments of Prout, or to the alcohol being administered with or without food, or even to individual peculiarities.

It was observed by Lavoisier and Seguin[2] as long ago as the end of the last century that the absorption of oxygen was increased by digestion, lowering of temperature, and the performance of work—and such has been shown to be the case by the investigation of modern observers, even though the amounts of oxygen obtained by Lavoisier differ both relatively and absolutely from those of the latter. It must always be a source of regret that Lavoisier did not describe the apparatus in which he placed Seguin, and by means of which he obtained the results just given, the genius of Lavoisier being as conspicuously manifested in the disposition of experimental detail, as in the establishment of grand generalizations. In all probability the apparatus used was essentially the same as in the case of the experiments performed upon the guinea-pig with the same object, that of determining the amount of oxygen absorbed and carbon dioxide exhaled in a given time, consisting in that instance of a bell-jar standing over a pneumatic trough, within which the animal was introduced and supported, after being passed up through the water of the trough, the oxygen being introduced as needed, in known quantities, and the carbon dioxide exhaled absorbed by alkali.

Recent researches[3] have shown that from 7 to 34 per cent. more oxygen is absorbed and from 7 to 31 per cent. more carbon dioxide expired during digestion than when fasting. This increase in the gaseous interchange during digestion appears to be due not only to the oxidation of the products of digestion and to the chemical processes incidental to the latter, but more especially to the activity of the muscular walls of the alimentary canal.[4]

The reverse effect, or the diminution in the exhalation of carbon dioxide in the absence of digestive activity through the depriving one's self, or an animal, of food, was also shown by Vierordt in his own person, by Spallanzani in the case of snails and silk worms, Marchand in frogs, and Bidder and Schmidt on cats.[5]

That muscular exertion increases the absorption of oxygen and expiration of carbon dioxide, has also been proved by a number of

[1] Milne Edwards, Physiologie, Tome ii., p. 536.
[2] Mem. de l' Acad. des Sciences, 1789, p. 575.
[3] Loewy, Pflüger's Archiv, Band 43, 1888, s. 515.
[4] Zuntz u. Mering, Ebenda, Band 32, 1883, s. 173.
[5] Milne Edwards, op. cit., p. 538.

observers. Thus, according to Vierordt,[1] during moderate exercise the carbon dioxide exhaled was increased in amount 19 c. c. (1.197 cubic inches) per minute, while Dr. Smith[2] found that in walking at the rate of three miles an hour, the exhalation of carbon dioxide in one hour was equal to that exhaled during two and three-quarter hours of repose with, and three and one-half hours of repose without food, and that the amount of carbon dioxide expired during one hour's work on a tread-wheel was equal to four and one-half hours of rest with and six hours without food. According to Pettenkofer,[3] while a man absorbed during rest 867 grammes of oxygen and expired 930 grammes of carbon dioxide, he absorbs during the performance of moderate work, 1006 grammes of oxygen and expires 1134 grammes of carbon dioxide. Hirn[4] states, however, as the result of experiments made upon several men that four times as much oxygen is absorbed during work as during rest.

The oxygen absorbed and carbon dioxide exhaled is also very much increased by involuntary excitement such as shivering for example, or to a greater extent even by voluntary effort.[5] It should be mentioned when muscular exertion is so excessive as to produce fatigue and exhaustion that the gaseous interchange is diminished and the same holds true of severe mental, as well as of bodily work.

It has been shown by Speck[6] that the maximum increase of oxygen and carbon dioxide is attained before that of exertion; that according to the position of the body, the increase for the same amount of work varies, that for a given amount of work the respiratory activity is greatest during the first part of the period of its performance; that the greater the increase of carbon dioxide expired, the less is the increase proportionally of oxygen absorbed, so that the carbon dioxide expired may contain more oxygen than is absorbed; that the quantity of air breathed is so intimately related to the carbon dioxide expired that the latter may be regarded as a measure of respiratory activity.

A natural inference from what has just been stated would be that during sleep the oxygen absorbed and carbon dioxide expired would be diminished, and such has been shown experimentally to be the case.[7] According to Smith[8] the amount of carbon dioxide expired during the night as compared with that expired during the day was in the ratio of 1 to 1.8. In hibernating animals like the marmot, for example, the amount of gaseous interchange is so small that little or no difference can be detected in the composition of the air in

[1] Cyclopædia of Anat. and Phys., Vol. iv., p. 348.
[2] Op. cit., p. 713. [3] Loc. cit.
[4] Exposition analytique et experimentale de la theorie mecanique de la Chaleur, 3d ed., Tome i., p. 35.
[5] Marcet, A Contribution to the History of the Respiration of Man. London, 1897, p. 43.
[6] Deutsches Archiv f. klin. Medecin, Band 45, 1889, s. 461.
[7] Milne Edwards, op. cit., Tome ii., p. 528. [8] Op. cit., p. 693.

which the animal has remained for three hours when in this torpid state. Indeed, according to Regnault and Reiset,[1] only one-thirtieth of the usual amount of oxygen is absorbed by the animal when in this condition.

The experiments of Vierordt[2] show that with slight diminution in the external temperature the amount of carbon dioxide exhaled by man is increased about one-sixth. Thus the external temperature being between 3 and 15 degrees C. (37.4° and 59° F.), the absolute amount of carbon dioxide exhaled per minute was 299.33 c. cm. (about 18 inches), while with the external temperature between 16 and 24 degrees the amount exhaled was only 257.81 c. cm. (15 inches). The result of Vierordt's experiments might have been anticipated, since a fall in the external temperature necessitates a greater production of heat, the high temperature of the body being maintained, and this implies a greater absorption of oxygen and consequently a greater exhalation of carbon dioxide. When we come to study the production of animal heat we shall see that one of the most striking contrasts between mammals and birds, as compared with remaining animals, is the power the former possess of generating heat to replace that lost through a fall in the external temperature. On the same principle as that just mentioned we should expect to find also that more carbon dioxide is exhaled in winter than in summer, there being a greater demand for the production of heat in the former case than in the latter. This has been shown to be the case more particularly by the researches of Dr. Edward Smith.[3] Thus the maximum amount of carbon dioxide is exhaled in January, February, and March, the minimum amount in July, August, and part of September; June and July being months of gradual diminution, October, November, and December of gradual increase. It should be mentioned in this connection, however, that animals, and probably also man, cannot at once adapt themselves as regards their respiration to sudden changes in temperature. Thus it was shown many years ago by W. Milne Edwards[4] that birds, for example, in winter would still consume the same amount of oxygen and exhale the same amount of carbon dioxide as usual, though the external temperature was artificially raised to that of summer heat. The inverse ratio existing between the temperature of the environment and the amount of carbon dioxide expired, just referred to, does not, however, always obtain, since Page and others[5] have shown that while the expiration of carbon dioxide diminishes with a rise of temperature from 4.4° C. (39.9° F.) to 14.3° C. (57.7° F.), with the attainment of the latter temperature the expiration increases. The effect of variations in the temperature of the body upon respiratory activity differs, however, from that of changes in the temperature of the environment,

[1] Op. cit., p. 411. [2] Op. cit., p. 551. [3] Op. cit., p. 703.
[4] De l'Influence des Agens Physiques sur la Vie. Paris, 1824, p. 200.
[5] Journal of Physiology, Vol. 2, 1880, p. 228.

respiratory activity being increased by a rise and diminished by a fall in the bodily temperature. Thus it has been shown by Colosanti[1] that while guinea-pigs absorb per kilogramme per hour 948.17 c. c. of oxygen, the temperature being 37.1° C. (98.7° F.), they absorb as much as 1242.6 c. c., the temperature being 39.7° C. (103.4° F.), and the same results have been obtained by experiments[2] made upon man during the condition of fever. It is well known also that the absorption of oxygen and the expiration of carbon dioxide undergo diurnal variations, the gaseous interchange rising after and falling before meals, the minimum being reached at night, the latter effect being partly due to the fact that more carbon dioxide is expired during sunlight than in darkness.

It is well known that the expiration of carbon dioxide is greater in a moist than in a dry atmosphere. Thus, according to Lehmann,[3] rabbits exhaled in a moist air the temperature being 38°C. (100° F.) 352 c. c. (22 cu. in.) of carbon dioxide, while in a dry air at the same temperature they expired only 240 c. c. (15 cu. in.).

It has been shown among others by Paul Bert[4] that any increase or diminution in barometric pressure acts upon living beings in increasing or diminishing the tension of the oxygen in the air they breathe, and the blood that circulates through their tissues, and that any increase or diminution in atmospheric pressure is unfavorable to living beings accommodated as they now are, to the present tension of atmospheric oxygen. Indeed, according to this observer, all life perishes in air sufficiently compressed. With a pressure simply of several atmospheres symptoms of narcotic poisoning set in similar to those experienced in breathing an atmosphere containing an excess of carbon dioxide, and due probably to the same cause, namely, an excess of carbon dioxide in the blood. With still higher pressure, 4 of oxygen—that is, 20 atmospheres, and upward—death takes place from asphyxia, accompanied with convulsions, as when caused by a deficiency of oxygen. Precisely the same effect is caused by the gradual diminution of atmospheric pressure. A sudden diminution, however, causes death, probably through the liberation of gases in the blood, which interfere mechanically with its circulation.

It might be supposed that an increase or diminution in the density of the air inspired, increasing or diminishing the amount of oxygen absorbed, must sooner or later influence the amount of carbon dioxide exhaled. That such is the case is shown by the experiments performed many years ago by Hervier and St. Leger[5] in which it was proved that with a slight augmentation of atmospheric pressure, the amount of carbon dioxide exhaled was increased.

[1] Pflüger's Archiv, Band 14, 1877, s. 125.
[2] Fubini and Benedicenti, Moleschott Untersuch., Band 14, 1892, s. 623.
[3] Physiological Chemistry, 1885, vol. ii., p. 144.
[4] La Pression Barometrique, 1878, p. 1153.
[5] Gazette des hôpitaux, 3me serie, 1849, Tome i., p. 374.

When the pressure, however, exceeds twenty atmospheres the production of carbon dioxide is diminished correspondingly to the diminished oxidation, and with still higher pressure it is entirely arrested, oxidation, according to Bert,[1] as we have seen, ceasing then altogether. With a diminution of atmospheric pressure the amount of carbon dioxide produced is also diminished.

The oxygen absorbed and carbon dioxide expired is necessarily influenced by the integrity of the nervous system since the nutritive processes in the tissues, as we shall see hereafter, are governed by the former.

Thus division of the motor nerve supplying a muscle reduces the consumption of oxygen 22 per cent., and the production of carbon dioxide 30 per cent., while section of the spinal cord diminishes the absorption by the tissues of oxygen 4 per cent., and the expiration of carbon dioxide 20 per cent., destruction of the cord causing the gaseous exchange to fall to a minimum.[2] In this connection it may be mentioned that the respiratory activity is much greater in hot-blooded than in cold-blooded animals, and that among the former the respiratory activity of birds is higher than that of mammals. Of the same species, *cæteris paribus*, the respiratory activity is greater in small than in large animals, the greater consumption of oxygen and production of carbon dioxide being due to the fact that the body surface is greater in relation to the body weight in the former, which entails therefore proportionally a greater loss of heat.

Having considered the amounts of oxygen absorbed and carbon dioxide expired, and the various conditions affecting the same, let us study now the ratio in which these gases are interchanged. As the volume of carbon dioxide produced through the combining of carbon with oxygen is equal to the volume of oxygen entering into its formation, it follows if all the oxygen absorbed in inspiration combines with carbon to form carbon dioxide, the volume of the carbon dioxide expired ought to be equal to that of the oxygen inspired. We have just seen, however, that the inspired air loses while in the lungs 4.78 vols. per cent. of oxygen, whereas it gains only 4.34 vols. per cent. of carbon dioxide. The ratio of the weight of oxygen contained in the carbon dioxide expired to the weight of the oxygen simultaneously absorbed was called by Pflüger[3] the "respiratory quotient" and on the above supposition the air respired being estimated in liters would be equal to

$$\begin{array}{lll} & \text{Grammes.} & \text{Liters.} \\ \text{Oxygen} & 6.205 & 4.34 \\ \text{Oxygen} & 6.834 & 4.78 \end{array} = 0.907$$

It will be observed that the respiratory quotient 0.90 is not the ratio of the weight of the oxygen absorbed to the weight of the carbon dioxide expired, but to the weight of the oxygen in that car-

[1] Op. cit., p. 1152. [2] Quinquaud, Compt. rend. Soc. Biol., 1884, p. 342.
[3] Pflüger's Archiv, Band 14, 1877, s. 472.

bon dioxide.[1] Since the latter occupies, however, the same volume as that of the carbon dioxide expired, the respiratory quotient is often expressed by the formula $\frac{CO_2}{O}$ which in the above case becomes $\frac{4.34}{4.78} = 0.907$. Inasmuch as of the oxygen absorbed part only is expired in the carbon dioxide, it is evident that part leaves the body in some other form than that of carbon dioxide, and which explains the fact that the volume of the expired air is slightly less than that of the inspired air. In speaking of the composition of the carbohydrates, it will be remembered that attention was called to the fact of the hydrogen present being in the proportion to form with the oxygen water. Suppose now that starch, a carbohydrate, be oxidized, the result would be the formation of carbon dioxide and the setting free of the water, the reaction being as follows:

$$C_6H_{10}O_5 + O_{12} = 6(CO_2) + 5(H_2O)$$

In an animal fed exclusively upon starch the respiratory quotient will be, therefore, unity, $\frac{6(CO_2)}{6(O_2)} = 1$, the volume of carbon dioxide expired being equal to that of oxygen absorbed, all of the latter combining with carbon. If, however, the same animal be fed upon a fat in which the hydrogen is in excess, more than sufficient to form water with the oxygen present, the absorption of oxygen and the oxidation of the fat would result in the formation of carbon dioxide and the setting free of the water, as in the first case; but as part of the oxygen absorbed would also combine with that part of the hydrogen in excess to form water, necessarily some of the oxygen absorbed would not reappear as carbon dioxide in the expired air, but as water. The reaction would be as follows, supposing olein to be the fat used:

$$C_{57}H_{92} + 2(H_6O_3) + O_{160} = 57(CO_2) + 2(H_6O_3) + 46(H_2O)$$

The respiratory quotient on a diet of fat would be, therefore, $\frac{57(CO_2)}{80(O_2)} = 0.712$.

If the animal is fed upon meat, the respiratory quotient is found to vary from 0.75 to 0.81 (according to the thoroughness with which the meat is digested), since after the urea was separated from the albumin the remainder of the meat would contain an excess of hydrogen, as in the case of fat, hence part of the oxygen absorbed in respiration would not reappear as carbon dioxide but as water, part of the oxygen combining with the carbon to form carbon dioxide and part combining with the hydrogen to form water.

These theoretical considerations[2] are fully confirmed by the experiments of Regnault and Reiset in which it was shown that in

[1] See p. 389.

[2] Op. cit.

animals fed upon starch the difference between the weight of the oxygen absorbed and that expired in the carbon dioxide was far less than in the case of animals fed upon fat or meat. On the other hand, in certain kinds of vegetable food, fruits, etc., the oxygen present being in excess more than sufficient to form with the hydrogen, water, it is to be expected that more oxygen will be expired in the carbon dioxide than absorbed in inspiration as shown, for example, in the oxidation of tartaric acid

$$C_4H_6O_6 + O_6 = 4(CO_2) + 3H_2O$$

The respiratory quotient on such a diet would be, therefore, more than unity

$$\frac{8(O)\text{vols.}}{5(O)} = 1.6.$$

The respiratory quotient being the ratio of the oxygen absorbed to the carbon dioxide expired must be affected by the same conditions that we have seen influence the gaseous interchanges and will vary according as the diet is a starvation one, mixed or limited to one particular kind of food. Thus, the respiratory quotient upon a starvation diet is equal to 0.68, upon a non-nitrogenous one 0.75, upon a nitrogenous one 0.90, upon a mixed one 0.94, no work being done and the oxygen absorbed and carbon dioxide expired, being such as given on page 440. Admitting that the part of the oxygen which is absorbed in inspiration and does not reappear in the carbon dioxide expired, combines with hydrogen to form water within the economy, the quantity so formed and exhaled is small as compared with the water taken in as such. Suppose that the hydrogen available for combustion is about 13 grammes (200 grains), the water formed would amount to only 117 grammes (1805 grains),

$$\begin{array}{cccccccc} H_2O & & H & & H_2O & & H \\ 18 & : & 2 & :: & 117 & : & 13 \end{array}$$

whereas, the water exhaled from the lungs of a man amounts on the average in twenty hours from 400 to 800 grammes[1] (6172 to 12344 grains).

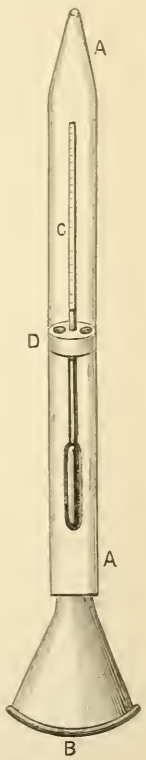
The manner in which the water exhaled by an animal is determined has already been referred to in the description of the respiration apparatus made use of for that purpose. In the case of man, however, the water exhaled can be more accurately determined by breathing into a curved tube, terminating in Liebig's bulb, filled with sulphuric acid and pumice-stone for the absorption of the water, the latter being estimated by the increase in weight.

The amount of water exhaled from the respiratory tract will be influenced, as in the case of inert bodies, by the amount of water present in the atmosphere, the temperature, and the pressure. Hence, the dryness of the throat and fauces experienced by persons

[1] Valentin, Lehrbuch der Physiologie, Band i., s. 527 ; Bunge, Lehrbuch, 1894, s. 272.

ascending into high altitudes through the loss of water due to the diminished pressure and great cold. The extent of the respiratory surface will influence also the amount of aqueous vapor exhaled. This is well seen in the diminution of the exhalation in old age, as shown by Barral,[1] the pulmonary cells becoming larger, a less extent of respiratory surface is offered. Finally, the amount of water exhaled is increased by the quantity of water taken in as drink, etc., and by the frequency of the respiration. In conclusion, it should be remembered that, if the ordinary conditions prevailing be reversed, water may be absorbed by the respiratory surface instead of being exhaled. The sudden gain in weight frequently observed in individuals who had not partaken of solid or liquid food, often referred to by writers on physiology,[2] is due, no doubt, to absorption by the lungs of the watery vapor of the atmosphere, rather than to cutaneous absorption, as sometimes supposed.

Fig. 207.



Apparatus for determining temperature of expired air.

The expired air differs from that inspired, not only in having lost oxygen and gained carbon dioxide and water, but in being warmer. It is due to this fact that the volume of the expired air is about one-ninth greater than that of the inspired air. If, however, both the expired and inspired air be reduced to standard temperature then the volume of the expired air will be found to be less, as already mentioned, than that of the inspired air. According to Grehant,[3] the air being inspired by the nares and having a temperature of 22° C. (71.6° F.), that exhaled by the mouth had a temperature of 35° C. (95° F.), as determined by a thermometer (Fig. 207, C) placed within the apparatus A, through which the air was expired, and which was uninfluenced by the external temperature. When the air was, however, inspired by the mouth, the air expired had a temperature of only 93°. The result of Grehant's observations differ a little from those of Valentin,[4] previously made. According to the latter observer, the external temperature being at 20° C. (68° F.), that of the expired air was 37.2° C. (90° F.). The temperature of the surrounding atmosphere has an important influence, however, upon that of the expired air; thus, according to Valentin, in winter the external temperature being — 10° C. (14° F.), that of the expired air was only 29° C. (85° F.).

[1] Ann. de Chimie, 1849, 3me ser., Tome xxv., p. 166.
[2] Carpenter's Physiology, p. 494.
[3] Journal de l'Anat. et de la Phys., Tome i., 1864, p. 546.
[4] Op. cit., s. 533.

Ammonia is undoubtedly exhaled from the lungs, being almost invariably found in the expired air. In fact, it is only absent at certain periods of the day, or during cold weather, as noticed by Richardson.[1] In certain conditions of the system, as in cases of uræmic poisoning, the amount of ammonia in the expired air is so great as to become very perceptible to the patient.[2]

Considerable difference of opinion has prevailed among physiologists as to whether nitrogen was absorbed or exhaled during respiration. The researches of Regnault,[3] Boussingault,[4] and Barral,[5] however, that, in mammals and birds at least, under ordinary circumstances, a small quantity of nitrogen is exhaled in respiration, equal to about one-fiftieth by weight of the oxygen absorbed. The reverse, however, appears to be the case with fishes, according to Humboldt and Provencal,[6] nitrogen being absorbed by those animals. According to recent researches[7] in the case of man no appreciable amount of nitrogen is either absorbed by or given out from the blood during respiration. In speaking of nitrogen, it may be incidentally mentioned that its mixture with oxygen as the air we breathe is obviously of advantage, since, on account of its great diffusibility, the air vitiated with carbon dioxide is readily renewed during respiration. A small quantity of organic matter, the nature of which is not thoroughly known, but, as we shall see, is, to a great extent, poisonous in character, is constantly present in the expired air. The presence of this organic matter can be shown through the putrefaction of the aqueous products of the expired air when condensed in a cool receiver, or through the putrefaction of a sponge saturated with the vapors exhaled by the lungs.

Many articles of food, like onions, garlic, alcohol, spirits of turpentine, drugs like camphor, musk, asafœtida, when absorbed by the blood and vaporized in the system, are exhaled by the lungs, being readily recognized by their odor in the expired air. That poisonous gases are also exhaled by the lungs is rendered very probable by the experiments of Bernard[8] and Nysten,[9] in which sulphuretted hydrogen and carbon oxide, so fatal when inhaled, were ejected into the veins without bad effect, being eliminated by the lungs as rapidly as they were taken up by the venous blood.

Many animals in which the respiration is of a feeble character, such as slugs, snails, certain kinds of fish, frogs, etc., continue to live in air from which the oxygen has been removed to a considerable amount.[10] Such, however, is not the case with animals whose respiration is very active, as in man. Any considerable diminution in the amount of oxygen in the surrounding air soon causes death.

[1] The Cause of the Coagulation of the Blood, p. 360. London, 1857.
[2] Lehmann, Phys. Chem., Vol. ii., p. 434. Philadelphia, 1855.
[3] Op. cit., p. 510.
[4] Chimie Agricole, pp. 1–24. Paris, 1854.
[5] Op. cit., p. 129.
[6] Milne Edwards, Physiologie, Tome ii., p. 599.
[7] Marcet, op. cit., p. 27.
[8] Substances Toxiques, p. 58. Paris, 1857.
[9] Recherches de Physiologie, p. 81.
[10] Milne Edwards, Physiologie, Tome ii., p. 626.

Just as a lamp goes out when the air feeding it does not contain more than about 17 per cent. of oxygen, so with the lamp of life its flame too dying out, respiration soon ceasing, if the amount of oxygen usually present in the atmosphere be diminished by absorption, or through dilution with some indifferent gas. In fact, air which has been breathed by man once should not be breathed again; such air having lost oxygen and gained carbon, if breathed twice, will give up but little oxygen to his economy. Indeed, as shown by Lavoisier,[1] air, having lost about 10 per cent. of oxygen, becomes absolutely irrespirable. Such is found to be the case in certain parts of mines where the air contains only that amount of oxygen. It is well known, also, that birds and mammals will suffocate in an atmosphere in which the amount of oxygen has been diminished to that extent. Thus, a mouse will die in six minutes, if confined in such an atmosphere, and a sparrow in an hour, if the oxygen be diminished to half that amount, or 5 per cent. It is not, however, the want of oxygen alone that causes death in breathing bad air, but the simultaneous increase of carbon as well. The ill effects experienced under such circumstances, such as headache, the sense of oppression, and even stupor appear to be due not to the carbon dioxide expired, but to the organic matter which it contains just referred to. This is shown by the fact that an atmosphere containing 1 per cent. of pure carbon dioxide exerts no deleterious effect upon the economy, whereas an atmosphere containing the same amount of carbon dioxide that has been expired is not only highly injurious, but soon becomes unendurable.[2] As the nature and amount of the organic matter expired to which the deleterious effects of breathing vitiated air is due are unknown, the carbon dioxide expired is taken as a measure of the same. Experience has shown that air fit to breathe should not contain more than 0.07 per cent. of carbon dioxide, and as 468 liters of carbon dioxide are expired in twenty-four hours it is obvious that the latter must be exhaled into 668304 liters of air if that air is to contain only 0.07 per cent. of carbon dioxide.

CO_2		Air.		CO_2		Air.
0.07	:	100	::	1	:	x.
		$x = 1428$ air.				
1	:	1428	::	468 lit.	:	x lit.
		$x = 668304$ lit. air.				

That is to say, every human being must be supplied with over 27,846 liters of air per hour in order that the CO_2 exhaled into it should not exceed in amount 0.07 per cent.

A room having a cubic capacity of 10 meters (352 cubic feet) would contain air enough to supply a human being enclosed within it with oxygen for twenty-four hours, but to prevent vitiation of the air the room would have to have a cubic capacity of 674 meters

[1] Deuxième, Mémoire sur la respiration mem. de Chemie, T. iv., p. 22.
[2] Pettenkofer, Med. Times and Gazette, 1862, p. 459.

(23,724 cubic feet) in order that at the end of the twenty-four hours the carbon dioxide exhaled into the air would not amount to more than 0.07 per cent.

In breathing in the open, where the atmospheric air is out of all proportion to that expired by any one individual, at no moment is any want of fresh air experienced. In our dwellings also, if properly constructed, a due supply of fresh air is maintained by the opening of the windows and doors, and the entrance of the outside air through the cracks, crevices, etc. In churches, theaters, lecture-rooms, barracks, prisons, hospitals, etc., however, where large numbers of people are congregated together, the proper supply of fresh air should never be left to chance. Indeed, this is now so well understood that in the ventilation of such buildings as the Chamber of Deputies and many of the hospitals in Paris, in the House of Commons in London, in the Philadelphia Academy of Music, etc., the air is continually renewed by means of fans worked by engines, etc., regard being paid to the fact that the air supplied is in reference not only to the amount of oxygen to be inspired, but also to the carbon dioxide, organic matter, etc., exhaled to be carried away, care being taken that the expired air does not mix with that to be inspired, and at the same time that drafts be avoided, the velocity with which the air passes through the chambers not being greater than from two to three feet per second.

Internal Respiration.

It has already been mentioned that while in external respiration the oxygen of the air passes into the blood and the carbon dioxide of the blood into the air, in internal respiration the oxygen of the blood passes into the tissues and the carbon dioxide of the tissues into the blood. The distinction between external and internal respiration is, however, a superficial one, since the blood is the means by which the oxygen of the air is indirectly carried to the tissues, and the carbon dioxide produced in the latter conveyed to the air. It should be remembered, however, that the blood, in addition to being the means of transportation of oxygen and carbon dioxide to and fro, as a tissue, consumes oxygen and produces carbon dioxide like other tissues. Thus it is well known that when readily oxidizable substances are introduced into the blood and the latter is transfused through the lungs or lung tissues more oxygen is taken up and carbon dioxide given off than by normal blood. There appears to be but little doubt that under ordinary circumstances the tissues give up to the blood similarly substances whose complete metamorphosis involves the consumption of oxygen and production of carbon dioxide.[1]

The relative avidity with which the tissues absorb oxygen is shown according to Quinquaud[2] in the accompanying table, 100 grammes

[1] Bohr and Henriquez, Comptes Rendus, Tome 114, 1892, p. 1496.
[2] Comptes Rendus Soc. Biologie, Tome ii., 1890, p. 28.

of tissue having been submitted in each instance to experiment for a period of three hours at a temperature of 38°C. (100°F.).

ABSORPTION OF OXYGEN BY TISSUES.

Muscle	23 c. c.	Spleen	8 c. c.
Heart	21 "	Lungs	7.2 "
Brain	12 "	Adipose tissue	6 "
Liver	10 "	Bone	5 "
Kidney	10 "	Blood	0.8 "

Oxygen in being absorbed by the tissues appears to enter into some form of molecular combination since its tension in the latter amounts practically, as already mentioned, to zero. That the carbon dioxide is formed to a great extent, at least, in the tissues, is shown by the fact that the amount of carbon dioxide in the fluids of the cavities of the body is greater than that in the blood, as shown below, and which can only be accounted for on the supposition that the carbon dioxide of these fluids passed into them from the tissues.

TENSION OF CARBON DIOXIDE IN FLUIDS OF BODY.[1]

	Mm. Hg tension.
Arterial blood	21.28
Peritoneal cavity	58.50
Acid urine	68.00
Cavity of intestine	58.50
Bile (gall bladder)	50.00
Hydrocele fluid	46.50
Lymph (thoracic duct)	34.00

The carbon dioxide produced in the tissues does not appear to be due in all instances to the immediate combination of the oxygen of the blood with the carbon of the tissues, since the latter will exhale carbon dioxide in the absence of oxygen, even in an atmosphere of hydrogen or nitrogen, carbon dioxide being produced in the tissues through the intra-molecular splitting of more or less broken-down substances, as well as by direct oxidation.

In concluding the subject of respiration attention may be appropriately called to the modifications of the normal respiratory movements or eupnœa, such as apnœa, absence of breathing; hypernœa or polypnœa, exaggerated breathing; dyspnœa, labored breathing; and asphyxia or suffocation. Difference of opinion still prevails among physiologists as to the cause of apnœa. Such facts as that apnœa can be produced by rapidly repeated respirations, that it is more marked after the breathing of pure oxygen, than that of air, and least marked when the air contains but little oxygen, have lead to the conclusion that the blood is saturated with oxygen in apnœa and that the necessity of respiration is not therefore felt in that condition. It has been shown, however, on the one hand[2] that apnœa can be produced by inflating the lungs

[1] Strassburg, Pflüger's Aerhiv, B. vi., s. 65.
[2] Head, Jour. of Physiology, Vol. 10, 1889, p. 43.

with hydrogen as well as with oxygen or air, and on the other, that apnœa cannot be produced either by inflation with hydrogen, oxygen, or air, after division of the pneumogastric nerves. The conclusion drawn from these experiments is that the rapid inflation of the lungs in exciting the terminal pulmonary filaments of the pneumogastric nerve, give rise to impressions, which, being transmitted to the medulla, inhibit the inspiratory impulses from the respiratory center. Polypnœa or hypernœa, in which the respiration is exaggerated, is due either to the respiratory center being excited, directly by the temperature of the blood being increased, or reflexly through stimulation of the cutaneous nerves by external heat. Dyspnœa, or deep labored breathing, may be due to either a deficiency in the oxygen or to an excess in the carbon dioxide of the air breathed. Dyspnœa, as caused by a deficiency of oxygen, is observed in cases where a man or animal is enclosed in a small chamber, or where pure nitrogen or hydrogen is breathed, the carbon dioxide being exhaled and carried off, even as rapidly as produced. Dyspnœa, as due to an excess of carbon dioxide, is produced when an animal is forced to breathe an atmosphere containing carbon dioxide to an amount of 10 volumes per cent., even though oxygen be present and in greater quantity than found in normal air. Dyspnœa, as caused by a deficiency in oxygen, differs from that caused by an excess in carbon dioxide. In the former case the inspirations are vigorous and frequent, the blood pressure rises and death, which is due to asphyxia, is preceded by convulsions; in the latter case the expirations are vigorous and slow, and death, which appears to be due to a kind of narcotic poisoning, is not preceded by convulsions. In cases of carbon dioxide poisoning the respiratory center appears to be excited, not only directly, but reflexly, through stimulation of the sensory fibers of the larger bronchi.[1] That form of dyspnœa, due to muscular activity, appears to be caused by substances whose nature is unknown, which are produced during muscular contraction, and passing into the blood excite the respiratory center. Cardiac dyspnœa is due to the blood being insufficient in quantity, hemorrhagic dyspnœa to the blood being poor in quality as well.

Asphyxia, from *ἀ*, primitive, and *σφυξις*, the pulse, literally a state of being without pulse, the condition brought about when the system is deprived of a due supply of air, whether suddenly by occlusion of the trachea, as in strangulation, or by slow suffocation through breathing in a confined space, manifests itself first by the breathing, both inspiratory and expiratory, becoming more frequent and deeper. This exaggeration of the breathing, or hypernœa, is soon succeeded by a condition of difficult breathing, or dyspnœa, the respiratory movements, at the same time, having become almost entirely expiratory in character, every muscle being brought into play that can contribute in any way to this effect. Sooner or later, the muscles of the whole body become involved in the convulsive

[1] Gado Zagari, Du Bois Reymond's Archiv für Physiologie, 1890, s. 588.

expiratory movements that follow. General convulsions then set in, which, after lasting a short time, are followed by collapse. At this stage the pupil is insensible to light, the cornea fails to respond to touch, breathing has become almost entirely inspiratory, and occurs only at long intervals. Finally, with a long and deep gasp death takes place, with the head thrown back, nostrils dilated, opened mouth, straightened trunk, and extended limbs. That the convulsions, which occur as dyspnœa passes into asphyxia, are due to the stimulation of the respiratory center of the medulla oblongata by the insufficiently arterialized blood circulating through it, is proved from the fact of such convulsions being absent if the spinal cord has been previously divided below the medulla, but being present if the part of the brain lying above the medulla only be removed. That these convulsions are, in fact, due to influences emanating from the medulla is still further shown by the rise in blood pressure that occurs during the development of asphyxia, and which is due to the constriction of the arterioles through the stimulation of the vasomotor center by the excessively venous blood, and by the fact that if the supply of blood to the brain be cut off by ligation of the vessels, convulsions, similar to those observed in asphyxia, follow. The facts just mentioned will become more significant, however, when the structure of the medulla and its influence upon the respiration and the circulation have been considered.

Owing to the constriction of the vessels at the periphery that obtains in asphyxia, offering an obstacle to the flow of the blood from the heart, while the increased respiratory movement favors the flow toward it, the heart soon becomes distended, and, finally, exhausted, though continuing to beat for a few moments after respiration has ceased. During the latter stage of asphyxia the blood pressure, therefore, not only falls, but the heart is weakened—that is, unable to empty itself of its contents. Hence, in post-mortem examinations of cases of death from asphyxia, if made before rigor mortis has set in, all the cavities of the heart will be found choked with blood. With the setting in of rigor mortis, however, the blood is expelled from the left side of the heart, the right remaining gorged with venous blood. The difference of opinion, that sometimes prevails, as to whether all the cavities of the heart are filled with blood in death from asphyxia, may be due, therefore, to the length of time intervening between death and the making of the post-mortem examination, having been different in the cases investigated. In this connection it may not be without interest to mention that Harvey[1] notices that, in cases of death from ordinary causes, the left side of the heart and arteries are found empty; whereas, in sudden death, as from syncope or drowning, the arteries, as well as the veins, are found full of blood. The duration of asphyxia varies very much in different animals, and according to the age of the animal. Thus, a dog will be asphyxiated by occlusion of the trachea in four or

[1] Works, p. 115. London, 1847.

five minutes, a rabbit in three or four minutes; whereas, as shown long ago by Buffon,[1] puppies just born can be submerged in warm milk for half an hour at a time, several times in succession, and yet recover; while, according to Legallois,[2] newborn rabbits lost consciousness only after having been kept thirteen minutes under water. Milne Edwards[3] refers to cases, interesting from a medico-legal point of view, where infants born asphyxiated were revived seven and even twenty-three hours afterward. The remarkable power that animals just born exhibit in resisting asphyxia depends principally upon the demand for oxygen being so slight at this time. In fact, at this early period of existence the newborn mammal is essentially a cold-blooded animal, it depending for its heat almost entirely on external warmth, the blood is still mixed through the foramen ovale being open, the circulation and respiration have not assumed the important *rôle* that they play in the adult, little or no muscular exercise is taken, most of the time being passed in sleep, hence but little oxygen is required. The connection between the deficiency in the circulation and the want of aëration just referred to, is also seen in cases of syncope in the adult, it being well known that a person in that condition can resist for some time the effects of asphyxia, the amount of oxygen consumed by the tissue being, of course, less in proportion as the circulation is slowed, the oxygen inspired will last, therefore, longer than usual.

[1] Natural History, Vol. iii., p. 337. London, 1797.
[2] Œuvres, Tome premier, p. 58. Paris, 1880.
[3] Op. cit., p. 559.

CHAPTER XXIV.

ANIMAL HEAT.

One of the most striking phenomena in the life of man, and in that of the hot-blooded animals generally (mammals and birds), and of plants, also, to a certain extent, which did not escape the attention of the ancients, is the almost constant temperature maintained by the body, notwithstanding the great extremes in temperature to which it may be subjected. Thus, whether one lives in a changeable climate, or passes from the genial atmosphere of the temperate regions into the extreme heat of the tropics, 53.3° C. (129° F.),[1] on the other hand, or into the intense cold of the arctics, — 57.7° C. (— 72° F.)[2] on the other, the temperature of the body varies, as we shall see, but little. If, however, the so-called cold-blooded animals, frogs, for example, be observed in this respect, a most notable difference becomes at once apparent, their temperature being, according to the circumstance, higher or lower than that of the surrounding water or air, and any rise or fall in it depending upon that of the latter. Thus, according to Landois,[3] the temperature of the water in which the frog is immersed being successively 2.8°, 20.6°, and 41°C., that of the stomach of the animal will be respectively 5.8°, 20.7°, 38.0°C., while if the animal be living in air at a temperature of 5.9°, 19.8°, and 40.4° C., that of the stomach will be at 18.6°, 15.6°, 31.7° C. Thus, as Hunter expressed it, warm-blooded animals have a certain permanent heat in all atmospheres, while the temperature of cold-blooded ones is variable with every atmosphere, hence the distinction of homoiothermal and poikilothermal animals introduced by Bergman,[4] and which being based upon the relation of the temperature of the body to that of the surrounding medium is a better one than that of hot- and cold-blooded animals, and which we have just incidentally alluded to.

Temperature of Animals.[5]

Name of animal.	Temperature.	Observer.
Aves—		
Chicken,	111° F. (43.8° C.)	Davy.[6]
Guinea fowl,	110	"
Thrush,	109	"
Sparrow,	108	"
Goose,	107	"
Screech owl,	106	"

[1] Jameson, British India, Vol. iii., p. 170. [2] Erman, Siberia, Vol. ii., p. 369.
[3] Physiologie, s. 393. Wien, 1883. [4] Gottinger Studien, Abth. i., s. 595.
[5] When not otherwise mentioned the temperature of the vertebrates was taken in the rectum. [6] Researches, Phys. and Anat., p. 161. London, 1839.

Name of animal.	Temperature.	Observer.
Mammalia—		
Hog,	105 (40.3° C.)	Davy.
Manatee,	104 abdomen,	Martine.[1]
Rabbit,	104 to 100,	Prevost and Dumas,[2] de la Roche.[3]
Sheep,	104	Davy.
Goat,	104	"
Rat,	102	"
Squirrel,	102	"
Cat,	102	"
Panther,	102	"
Dog,	102	"
Monkey,	101	"
Porpoise,	100 liver,	"
Ox,	100	"
Elephant,	99.5	"
Horse,	99.5	"
Reptilia—		
Green snake,	88.5	"
Tortoise,	87 œsophagus,	"
Iguana,	82.5	"
Alligator,	69	Jones.[4]
Amphibia—		
Frog,	64	Davy.
Pisces—		
Trout,	58	"
Eel,	51	"
Articulata—		
Beetle,	77 surrounding air 76°,	"
Cockroach.	75 " " 74°,	"
Mollusca—		
Oyster,	Temp. same as sea, 82°,	"
Snail,	76.5 surrounding air, 76.25°,	"
Echinodermata—		
Star fish,	6–10° F. above temp. of sea (66.3°)	Valentin.[5]
Sea urchin,	5–10 " " " (66.7)	"
Sea cucumber,	6–10 " " " (67.6)	"
Vermes—		
Leech,	1 " " of air (56.)	Hunter.[6]
Celenterata—		
Anemone,	5–10 " " of sea (69.4)	Valentin.
Jelly fish,	7–10 " " " (72.5)	"
Ponfera—		
Sponge,	Same as sea (68.3° F.)	"

[1] Essays, Medical and Philos., 1740, p. 337.
[2] Annales de Chim. et de Phys., 2e serie, Tome xxiii., p. 64, 1823.
[3] Journal de Physique, lxxi., p. 298, 1810.
[4] Investigations, Chem. and Physiol., Smith Contrib., 1856.
[5] Repertorium für Anat. und Phys., Vierter Band, s. 359. Bern, 1839.
[6] Works, ed. by Palmer, Vol. iv., p. 147. London, 1835.

As the temperature differs often in individuals of the same species, and according to the biological conditions influencing the animal at the moment of observations, and further, as the number of observations are comparatively limited, any results, such as offered in the above résumé can only be accepted as giving approximately the average temperature in animals.

Of all animals, birds have the highest temperature, that of the chicken, for example, according to Davy[1] being as high as 43° C. (111° F.), a slightly higher temperature, according to Pallas,[2] even being found in certain small birds. Among mammals the temperature of the rabbit is noteworthy, amounting to 40° C. (105.8° F.). On the other hand the temperature of fishes, with some exceptions, is not usually more than 0.5° C. (0.9° F.) higher than that of the water in which they life, whilst among the invertebrata,[3] as in the case of mollusks, star fish, jelly fish, anemone, the excess of the temperature over that of the surrounding medium may be even less, amounting often to no more than 0.2° C. As an exception to the last statement and interesting in this connection may be mentioned the considerable amount of heat developed by bees and ants when swarming. Although a great number of observations have been made, some difference of opinion still prevails as to what constitutes the average normal temperature in man. This, however, is readily understood when, as we shall presently see, the temperature of the body not only varies considerably in different situations, but according to numerous circumstances; among others may be here very appropriately mentioned especially the manner in which the thermometrical observations should be made. It is of the highest importance, not only that the part of the body selected for taking the temperature should be mentioned, but that the thermometer used in making the observation should be a standard one.

The metastatic thermometer of Walferdin (Fig. 208) is a convenient form of instrument since by means of it a variation of $\frac{1}{100}$ of a degree, Centigrade, corresponding to a millimeter in length of the mercury, can be accurately determined. The instrument, however excellent it may be at the time obtained, should nevertheless be constantly tested.

Further, in using the thermometer it should be so ap-

FIG. 208.

Walferdin's metastatic thermometer. (LANDOIS.)

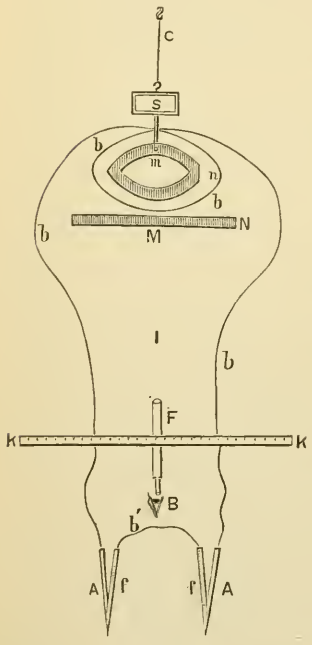
[1] Researches, Phys. and Anat., p. 186. London, 1839.

[2] Gavarret, De la Chaleur Produite par les Etres Vivants, p. 94. Paris, 1855.

[3] Milne Edwards, Physiologie, Tome neuvieme, 1863, p. 13.

plied that the part whose temperature is to be determined completely surrounds the bulb of the instrument; hence, of all parts of the body, the rectum is that which is best adapted for thermometrical observations, the instrument being inserted to a depth of at least 5 cm. (2 in.). On account, however, of being more convenient, the axilla is frequently made use of in determining the temperature of the human body. It must be remembered in that case then that the temperature is usually $\frac{5}{10}$ to 1 degree lower than that of the rectum. The tongue and vagina are also frequently made use of in taking the temperature. Apart from individual idiosyncrasies the difference of opinion that prevailed more particularly among the older physiologists with reference to the temperature of man is largely due to neglect of the precautions just referred to. If from the nature of the case, on account of the size of the cavity to be examined, etc., the application of a thermometer is inadmissible, thermo-electric needles are then made use of in determining the temperature. Even greater precautions must be taken than when the observation is made in the usual way on account of the delicacy of the apparatus, as slight a variation as the $\frac{1}{4000}$ of a degree having been determined by such. Thermo-electric needles (Fig. 209, A f, f A) are usually made of iron and German silver, each needle consisting of iron (f) and silver (A), soldered together at and near their points, and the two so disposed as to constitute together an element. The iron wires being in the middle, and the silver ones externally, if the latter are connected with each other through a galvanometer (M), a circuit is formed. The deviation of the needle will then indicate the temperature of the part examined through the electricity developed by the contact of the needles with the heated surface. The wires are, of course, except where soldered together, carefully isolated, and where held, are covered with silk and varnish. When the difference in the temperature of two parts of the body is to be determined, the two needles are imbedded in the parts, and the intensity of the current measured and the amount of heat determined, the relation between the deviation of the needle and the amount of heat producing it having been previously experimentally determined. This can be accomplished by immersing the needles with delicate thermometers attached, in oil baths

FIG. 209.



Thermo-electric needles. (LANDOIS.)

differing in temperature, for example, by one degree C. The deviation of the galvanometer needle will then indicate a difference in temperature of one degree C. Suppose, further, that as measured by the scale, the deviation of the galvanometer needle amounts to 150 mm., then $\frac{1}{150}$ of a degree C. of temperature is indicated by a deviation of 1 mm. of the needle. If absolute temperature be required, then one needle is applied to a surface maintained at a known temperature, and the other to that whose temperature is to be determined, or the known temperature can be gradually reduced until there is no deviation of the needle. The opposite currents being then equal the heat producing them must be equal—that is, the unknown heat is equal to the known. It was by means of such a thermo-electric apparatus that Becquerel,[1] and Breschet determined the temperature of the biceps muscle under different external conditions, to be referred to in a moment, and Nobili and Melloni[2] proved that the internal temperature of insects was slightly higher than that of the surrounding atmosphere. Among the most reliable observations that have been made with reference to determining the average temperature of the human body may be mentioned those of Hunter,[3] 37.2° C. (98.9° F.), Davy,[4] 37.3° C. (99.1° F.), Wunderlich,[5] 37° C. (98.6° F.), Jurgensen,[6] 37.2° C. The mean of Jurgensen's observations, it will be observed, is the same as that of Hunter, a confirmation of the accuracy with which that great physiologist investigated the subject of animal heat as all other biological phenomena. The results of Jurgensen's experiments are most important, both on account of their number and the length of time over which they extended. They consisted in reading off at intervals of five minutes the indications of a thermometer permanently retained in the rectum, and extended over three days. The mean obtained by Jurgensen was 37.2° C. (98.9° F.), which we will consider as being the average normal temperature of the human body, although variations between 37° and 38° C. (98.6° and 100.4° F.) may occur within the limits of health.

Among the various conditions that modify the normal temperature may be mentioned, in addition to the influence of the part of the body examined, to which we have already incidentally alluded, that exerted by age, sex, the time of day, food, muscular and mental work, external temperature, etc. To the consideration of these let us now turn.

[1] Ann. des Sciences Naturelles, 2d ser., 1835, t. iii., p. 269.
[2] Ann. de Chimie et de Physique, 1831, t. xlviii., p. 208.
[3] Works of John Hunter, ed. by J. F. Palmer, vol. i., p. 289. London, 1835. Phil. Trans., 1844, p. 61.
[4] Researches, Phys. and Anat., 1839, vol. i., p. 162.
[5] Op. cit., s. 92.
[6] Deutsche Archiv klin. Med., Band iii., s. 166.

Age and Sex.

According to Andral,[1] Bärensprung,[2] and others, the temperature before birth, as well as immediately afterward, is slightly higher than that of the mother; but as the newborn child possesses but little power of resisting external cold, its temperature soon falls, within two hours, perhaps, from 37.8° to 35.2° C. (100.04° to 95.3° F.). Hence the importance of providing for the infant sufficient warmth by suitable means, and to the neglect of which the death in many instances is undoubtedly due. Immediately after birth the temperature of the infant taken in the rectum is between 37.5° and 37.8° C. (99.5° and 100.04° F.), falling after the first bath to 37° C. (98.6° F.) and even lower, while during the next ten days it varies between 37.25° and 37.6° C. (98.9° and 99.6° F.), being notably increased by screaming, etc. During the period intervening between early infancy and the age of puberty the temperature falls about 0.2° C. (3.6° F.), and from there on till adult life falls about 0.2° C. still more, the normal temperature or 37.2° C. (98.9° F.) being then reached. After sixty years of age the temperature begins to rise again, and at eighty years has again reached that of the newborn child. This rise in temperature in old age is probably due to the diminished circulation of the anæmic skin, since it cannot be supposed that the production of heat has been increased. As a general rule, sex has no appreciable influence upon the temperature of the body. According to Ogle,[3] however, the temperature of the female appears to be slightly higher than that of the male.

Diurnal Variations.

The temperature of the body, like the frequency of the pulse, respiration, and exhalation of carbon dioxide, exhibits periodical variations. From the numerous observations of Davy, Hallmann, Gierse, Bärensprung, Lichtenfels, Frohlich, Damrosch, Ogle, Liebermeister, Jurgensen,[4] it appears that the temperature of the body increases very quickly from 6 A. M. to 11 A. M., but from that time forward increases more slowly, reaching a maximum between 5 and 6 P. M. About 7 in the evening the temperature begins to fall, reaching the minimum about 5 A. M., the difference being in 24 hours usually about 1° C. (1.8° F.), though it may amount to as much as 2° C. (3.6° F.).

Climate seems to influence the time of day at which the maximum and minimum temperatures occur, the minimum being reached, according to Davy, in England by midnight, but in the tropics not before 6 or 7 A. M.

[1] Compt. Rend., T. lxx., p. 825.
[2] V. Bärensprung, Arch. f. Anat. u. Phys., 1851, s. 138.
[3] Kirke's Physiology, 10th ed., p. 255. Phila., 1881.
[4] Rosenthal, die Physiologie der thierischen Wärme in Hermann, op. cit., Vierter Band, s. 322.

DIURNAL VARIATION IN TEMPERATURE.[1]

	Hour.	Barensprung.	Davy.	Hallmann.	Gierse.	Jurgensen.	
	5	.... Cent.	....	....	....	36.7	36.6
	6	36.68	....	....	....	36.7	36.4
	7	....	36.94*	36.63	36.98	36.7*	36.5*
A. M.	8	37.16*	....	36.80*	37.08*	36.8	36.7
	9	....	36.89	....	....	36.9	36.8
	10	37.26	....	37.36	37.23	37.0	37.0
	11	....	36.89	....	....	37.2	37.2
M.	12	36.87	....	....	....	37.3*	37.3*
	1	36.83	....	....	37.13	37.3	37.3
	2	....	37.05	37.21	37.50*	37.4	37.4
	3	37.15*	....	....	37.43	37.4*	37.3*
	4	....	37.17	....	....	37.5	37.5
	5	37.48	37.05*	37.31	37.43	37.5	37.5
	6	....	36.83	....	37.29	37.5	37.6
	7	37.43	36.50*	37.31*	30.00	37.5*	37.6*
P. M.	8	....	....	....	....	37.4	37.7
	9	37.02*	....	....	....	37.4	37.5
	10	....	....	....	37.29	37.3	37.4
	11	36.85	36.72	36.70	36.81	37.2	37.1
	12	....	....	....	....	37.1	37.4
	1	36.85	36.44	....	....	37.0	36.9
	2	....	....	....	....	36.9	36.7
	3	....	....	....	....	36.8	36.7
	4	....	....	....	....	36.7	36.7

Asterisk signifies that food was taken.

Supposing with Jurgensen, that the day temperature begins at 6 A. M. with 36.4° C., and ends at 8 P. M. with 37.7°, the duration of the former with a usually mean temperature of 37.3°, exceeds the latter with a mean of 36.9° by four hours, the average temperature for the whole day, being, as already mentioned, about 37.2° C. (98.9° F.). As might be expected, Debczynski[2] finds that persistent night work reverses the rhythm of the variations of temperature, the thermometer standing highest in the morning (37.8°), instead of in the evening (35.3°).

Food.

As in the long run the heat, as we shall see, is due to the combustion of substances taken into the body as food, it follows that the production of heat is intimately associated with that of nutrition. Inasmuch, however, as it is not until the last stage of inanition in the starving man or animal that the temperature notably falls, it having been previously maintained in the absence of food through the combustion of the tissues, it is not to be expected that in health the mere taking of food will influence the temperature to any great extent, since the fuel, so to speak, is ordinarily consumed as rapidly as supplied, and when deficient is made up at the expense of the tissues. For example, very hot drinks increase the temperature but little. Suppose, for example, a man weighing 60 kilogrammes (132 pounds) drinks a kilogramme (2.2 pounds) of water at 50° C.

[1] Landois, op. cit., s. 406. [2] Virchow u. Hirsch, Jahresber., 1875, Band i., s. 248.

(122° F.), the temperature of the whole body—supposing it to be 37.2° C. (98.9° F.) and having the same specific heat as water—would be increased only about 0.2° C. (0.3° F.). It must be remembered in this instance, as in many others, that the effect of taking a hot drink is not so simple as may at first appear, since the circulation being increased by it the loss of heat through evaporation will be increased. The one effect neutralizing to a certain extent the other, the full effect of the drink as regards elevation of the temperature is not therefore experienced. Even if the drinks contain specific substances, such as tea, coffee, alcohol, etc., the temperature of the body is diminished only two- or three-tenths of a degree C. It is possible that the loss of heat experienced in the taking of alcohol is not only due to the quickened circulation, but to a paralyzing effect exerted upon the vasomotor nerves of the skin, whereby a greater quantity of blood being conveyed to the surface than usual, more heat is consequently given off and so lost. On the other hand, while the effect of cold drinks, etc., is to diminish the temperature of the body, the diminution is also very slight, amounting usually to but a few tenths of a degree C. Thus, according to Lichtenfels and Frolich, Winternitz, and others,[1] drinks at a temperature of 18°, 16.3°, and 4.6° C., reduced that of the body in the first two instances within 6 minutes after taking them 0.1°, 0.4°, and in the last in 70 minutes 1.4° C. Further, as in the digestion of solid foods, heat is required to assist the chemico-physical changes, it might be expected that as part of the heat becomes latent, the temperature of the body would be slightly diminished temporarily after taking the food, even though the temperature should be increased later through further oxidation. That such is the case seems to be shown by the experiments of Vintschgau and Dietl,[2] made upon a dog with gastric fistula, in which the temperature of the food introduced, and which differed but little from that of the body, first fell and then rose. From what has just been said, however, of the compensating power exercised by the economy, whether food be taken or withheld, it would be inferred that the influence exerted by the taking of food upon the daily variations must be very slight, if any. Indeed, the variations in temperature that are observed after meals, as a matter of fact, occur whether food be taken or not. The most, indeed, that can be said is that if a meal be taken late in the day the diminution in temperature, characteristic of that period, is somewhat put off. Indeed, it is not until shortly before death caused by inanition or starvation, for the reasons already given, that the temperature is notably diminished.

Muscular, Mental, and Glandular Action.

We shall soon see, in our study of muscular action, that at the moment of muscular contraction a considerable amount of heat is set

[1] Rosenthal, op. cit., s. 325.
[2] Sitz. d. Weiner Acad. Math.-Natur. u. Cl., 2 Abth, ix., s. 697, 1870.

free—indeed, probably three-fourths of the heat developed is produced in the muscles. Thus, according to Davy,[1] the temperature of the room being 66° F., that of the feet 66°, under the tongue 98°, and of the urine 100°; after a walk in the open air at 40° the temperature of the feet was 96.5° and the urine 101°, that under the tongue being unchanged. Indeed, daily observation as well as special experiments teaches us that our whole body is warmed by muscular exercise. Further consideration, however, will show that the body is not as much heated as one would be led to expect from the amount of heat developed under the circumstances, and from the rapidity with which the temperature of the body falls to the normal with the cessation of the exercise, it is evident that as fast as the heat is developed it is as rapidly radiated away or lost as some other mode of energy. The influence of muscular exercise in elevating the temperature of the body is also well seen under certain pathological conditions; the temperature in tetanus, for example, rising, according to Wunderlich,[2] as high as 44.75° C. (111.2° F.). It should be mentioned, however, that this great rise in temperature can hardly be attributed entirely to muscular action, since in all probability, at the same time, other influences come into play, such as the action of the vasomotor nerves, which in constricting the vessels of the skin will diminish the usual loss of heat due to radiation and evaporation.

Nervous-like muscular activity is also accompanied with the production of heat. Thus, according to Davy,[3] during the reading of a work, in England, demanding attention, the temperature of the body was increased 0.5° F. Mental effort in the tropics is accompanied by a still greater production of heat, amounting, in some instances, to more than 2° F., as in the giving of a lecture, for example; in the latter case some of the heat was probably due to the muscular action involved. Lombard[4] has also determined, by means of delicate thermo-electric apparatus, local increase of temperature in the head resulting from mental effort. Schiff[5] has also shown that the action of the nerves, as well as that of the brain, is accompanied with the production of heat. In all instances, however, the amount of heat produced, at least that appearing as such, is a small part of the heat produced, as in the case of muscle being converted, as we shall see hereafter, into other modes of energy.

Glandular action is also accompanied by the production of heat due to the chemical activity incidental to secretion. Thus, according to Ludwig and Spiess[6] the temperature of the saliva secreted during stimulation of the chorda tympani is 1 to 1.5° C. higher than that of the blood of the carotid artery of the same side. We have already called attention to the fact of the temperature of the blood

[1] Phil. Trans., 1844, p. 63. [2] Op. cit., s. 400. [3] Phil. Trans., 1845, p. 443.
[4] Experimental Researches on the Regional Temperature of the Head. London, 1879. [5] Archiv de Phy. Normal et Path., 1870, pp. 5, 198, 323, 421.
[6] Wien. Sitzb., Band xxv., 1857.

of the hepatic vein being higher than that of any other part of the body, due, in part at least, to the size and constant activity of the liver.

Surrounding Temperature.

Any consideration as to the temperature of man or animal would naturally suggest the influence exerted by that of the surrounding atmosphere, and concerning which there was, at one time, much difference of opinion. So distinguished a teacher as Boerhaave, for example, advocated [1] that neither man nor any animal that breathes by lungs can live in an atmosphere the temperature of which is as high as that of their own bodies and cites [2] in support of this view the experiments performed at his request, by Fahrenheit and Provost, which consisted in placing a sparrow, a cat, and a dog in a sugar-baker's oven, heated to 146° F., and in which it was found they soon died. Notwithstanding the result of these experiments, the great Haller, basing his opinion upon the testimony of Lining Adamson, and other travelers, as to the intense heat that prevailed in certain parts of this country, South Carolina, Senegal, and elsewhere, held [3] in opposition to the view entertained by Boerhaave that man could not only live in an atmosphere 16°, but even 28°F., higher than that of the blood. About this time important observations bearing upon this question were made by Franklin and Governor Ellis. In a letter dated London, June 17, 1758, in referring to a hot Sunday passed in Philadelphia, in June, 1750, Franklin [4] recalls that, during the day, when the thermometer was at 100° F., in the shade, his body never grew so hot as the air surrounding it, or the inanimate bodies immersed in the same air, and, with his usual acuteness, accounts for the body being kept cool under such circumstances by continual sweating, and by the evaporation of that sweat.

Within a month of the same year—that is, in July 17, 1758—Governor Ellis, in a letter to his brother in London, called attention particularly to the fact that, while in Georgia, a thermometer suspended from under an umbrella which he carried during a walk of one hundred yards registered 105° F., the temperature of his body was only 97°. The letter of Governor Ellis being communicated to the Royal Society [5] was thereby at once insured a wide circulation; that of Franklin, though written first, was not made public, however, till afterward.[6] Shortly after the observation of Ellis, just referred to, it was ascertained by Tillet,[7] in experimenting with a baker's oven, that the young women in attendance were accustomed to remain in it for a few minutes even when at a tem-

[1] Prælectiones Academiciæ, Göttingen, 1740, Vol. ii., p. 211.
[2] Elementa Chemiæ, Lipsæ, 1732, Tomus Primus, p. 238.
[3] Elementa Physiologiæ, p. 37. Lausanne, MDCCLX.
[4] Works, Vol. iii., p. 301. Phila., 1809.
[5] Phil. Trans., 1759, Part ii., Vol. l., p. 755.
[6] Journal de Physique, 1773, Tome ii., p. 453.
[7] Mem. de l'Acad. des Sciences, 1764, Tome lxxxi., p. 188.

perature of 126.6° C. (260° F.). In one instance Tillet, anxious for the safety of the woman, requested her to come out, but she assured him she felt no inconvenience, and remained in the oven for ten minutes, the latter having a temperature of 137.7° C. (280° F.); indeed, on her coming out, beyond the flushing of the face, there was nothing especially noticeable. While the facts just referred to excited considerable interest at the time, it was not till some years later, however, that any further experiments were performed with the object of ascertaining the effect of heated air upon the temperature of the body. In 1774, the subject, however, was taken up again by Fordyce, who, together with Blagden, Solander, Banks, and others, experimented upon themselves, either in a room heated with flues, and upon the floor of which boiling water was poured, or in rooms heated with flues only. The result of these experiments, as described by Blagden,[1] may be summed up as follows:

In the room containing vapor Fordyce was able to bear for 10 minutes a temperature of 43.3° C. (110° F.), 20 minutes 48.8° C. (120° F.), and for 15 minutes a heat gradually increasing from 53.8° to 54.4° C. (119° to 130° F.). In these experiments, it is said, that the temperature under the tongue and of the urine did not rise higher than 37.7° C. (100° F.). In the room heated with flues only, and containing dry air, Fordyce, together with Blagden and Banks in the room, could stand, however, a higher heat than in the former instance, supporting for ten minutes a temperature of 92.2° C. (198° F.). Shortly after these experiments it was ascertained by Dobson,[2] from observations made in the sweating-room of the Liverpool Hospital, that individuals could stand for periods between 10 and 20 minutes a temperature, if the air be dry, of between 94.4° and 106.6° C. (202° and 224° F.). Fordyce, himself, as mentioned in a subsequent paper by Blagden,[3] was able to endure for 8 minutes even as high a temperature as 127° C. (260° F.), the uncomfortable feeling experienced quickly passing away with the breaking out of a profuse sweat. The immunity possessed by persons habitually exposed from time to time to a dry atmosphere, having a temperature even higher than that to which Fordyce, Blagden, etc., were subjected, is undoubtedly due, in a great measure at least, as Franklin supposed, to the cold produced through the evaporation of the cutaneous perspiration and pulmonary exhalation. In this way can be explained how the workmen of the sculptor Chantry went into a furnace having a temperature of 171° C. (340° F.), and Chabert, the fire king, into one at between 204° and 315.5° C. (400° and 600° F.). Indeed, the salutary effect, under such circumstances, of keeping the temperature down by evaporation was fully recognized by Fordyce and Blagden,[4] and proved by them in the following way: Two similar earthen vessels, one containing water only and the other an equal

[1] Phil. Trans., Vol. lxv., 1775, Part i., p. 111.
[2] Idem, p. 463.
[3] Idem, p. 484.
[4] Op. cit., p. 491.

quantity of water, with a bit of wax, were put upon a piece of wood in the heated room. In an hour and a half the pure water was heated to 60° C. (140° F.), while that containing the wax had acquired a temperature of 66° C. (152° F.), as the wax in melting had formed a film upon the surface of the water, and thereby had prevented evaporation. Further, it was observed that the pure water never came near the boiling point, but if a small quantity of oil was dropped into it, as had been done before with the wax, finally the water in both vessels boiled briskly. The effect of sweating in keeping down the bodily temperature is daily seen in the taking of Turkish as compared with Russian baths, an equally high temperature being much better borne in the former, on account of the air being dry, than in the latter, where the air is moist. The profuse perspiration induced through hot baths has long been a matter of comment; as early as the first half of the last century Le Monnier,[1] in speaking of the natural hot baths at Baregas, with a temperature in the hottest part of 44.4° C. (112° F.), observes that the sweat poured down from his face after remaining in it 8 minutes, and that after that time he was obliged to leave the bath, with reddened and swollen skin, and greatly increased pulse through violent attacks of vertigo. The conclusion drawn from the different experiments of Fahrenheit and Provost, Tillot, Fordyce, and Blagden, etc., that we have just described, was that man could not only exist in an atmosphere having a higher temperature than that of his own body, but that the latter remained unchanged, even when that of the surrounding atmosphere was greatly increased, notwithstanding that in an experiment with a dog the temperature was found by Fordyce to increase. It would appear, however, without doubt, from later observations, that with an increase in the temperature of the surrounding air there is an increase in that of the body. Thus, in the experiments made by De la Roche[2] and Berger, it was found that, after remaining 15 minutes in a vapor bath, with a temperature varying between 37.5° and 48.8° C. (99.5° and 119.8° F.), the temperature in the mouth was increased 3.1° C. (5.5° F.), while in dry air, but at a temperature of 80° C. (176° F.), the temperature was increased about 5° C. (9° F.). According to Davy[3] also, who made a great number of observations in different parts of the world, the mean temperature of the body in the tropics is about 1° F. higher than in England. Such a variation has been held by Boileau,[4] for example, as abnormal, and as an indication of a slight disturbance in the system due to change of climate, and to which certain delicate persons are liable. The observations of Eydoux[5] and Souleyet, made during the voyage of the "Bonite," and of Brown-Séquard,[6] to the Isle of France, though less in

[1] Mem. de l'Acad. des Sciences, 1747, Tome lxiv., p. 271.
[2] Thèses de l'ecole de médecine de Paris, 1806, No. 11. Journal de physique, 1776, Tome vii., p. 57.
[3] Philos. Transact., 1850, p. 437.
[4] Lancet, 1878, p. 413.
[5] Comp. Rend., 1838, Tome vi., p. 456.
[6] Journal de Physiology, T. ii., p. 554.

number than those of Davy, so far as they go, confirm the result obtained by that reliable observer. Davy[1] also showed, from a number of observations, that the mean temperance of the air being 15.5° C. (60° F.), that of the body was 36.7 C. (98.28° F.), whereas, if the temperature of the air rose to 26.6° C. (80° F.), the temperature of the body rose to 37.5° C. (99.67° F.).

The temperature of individual portions of the body has been shown to increase with that of the surrounding medium, as well as that of the whole body. In an experiment of Becquerel and Breschet,[2] for example, where the biceps muscle was surrounded for 15 minutes by water at a temperature of 42° C. (107.6° F.), the temperature, as determined by their thermo-electric apparatus was increased two-tenths of a degree. The rise in temperature, through increase of heat in the surrounding atmosphere, can be well shown in animals. Thus, according to Rosenthal,[3] the temperature of a rabbit rose from the normal, 38° C. (104.4° F.) to 45° C. (113° F.), while the external temperature was increased from 32° to 40° C. (89.6° to 104° F.), death taking place at the latter temperature. Essentially the same result was obtained in the experiments of De la Roche and Berger with a guinea-pig. According to these observers, as well as Rosenthal, an increase in the temperature of 6° to 7° C. (10.8° to 12.6° F.) above the normal, however brought about, is fatal to all animals. It would appear from these experiments as well as the earlier ones of Provost and Fahrenheit, that large animals bear a high temperature better than small ones, probably because, in the latter, a greater quantity of heat is produced relatively and more quickly. Thus, in the experiments of Fahrenheit, already referred to, of the three animals placed in the oven the sparrow died in 8 minutes, whereas the dog and the cat survived 28 minutes. According to De la Roche and Berger, a mouse died in 32 minutes, the temperature being increased from 57.5° to 63.7° C. (135° to 146.6° F.), while a guinea-pig survived 1 hour and 25 minutes, the temperature rising from 62 to 80° C. (143.6° to 176° F.); a young ass, however, though weak at the end of the experiment, successfully resisted for nearly three hours a temperature increased from 60° to 75° C. (140° to 167° F.). In the case of man, in certain pathological conditions, as in typhoid and typhus fever, the temperature of the body may rise to 40.5° and 41.1° C. (105° and 106° F.), and yet recovery take place. The highest temperature yet observed in man, and ending in recovery, was in a case of injury to the spine, reported by Dr. J. Teale,[4] in which the thermometer registered 50° C. (122° F.). The elevation in temperature in sunstroke, 40° to 44.4° C. (104° to 112° F.), is also very considerable; in such cases, however, the high temperature is to be attributed, in part at least, not only to the effect of exposure to the sun's heat, but also to the exercise taken incidental to the

[1] Researches, Phys. and Anat., p. 163.
[2] Ann. des Sciences Nat., 1838, p. 271.
[3] Op. cit., s. 337.
[4] Lancet, March 6, 1875.

character of the occupation of those usually attacked, such as field and street laborers, soldiers, etc.

Inasmuch, as we have seen, through the free action of the skin, and with proper precautions taken as regards exercise, food, clothing, etc., man can live in an atmosphere the temperature of which is much higher than that of his body, it might naturally be supposed that through similar compensating agencies intense cold can be equally well resisted, if not better than intense heat. Such, indeed, experience proves to be the case, the temperature of the body of man, even when exposed to the intense cold of the Arctic regions, is almost the same as in the temperate ones, since the amount of heat generated absolutely, is greater on account of the quantity and quality of food, and relatively so, from the fact of the clothing, etc., being of such a character as to retain the heat produced. In animals the latter protective effect is provided for by their fur, wool, feathers, etc., as the case may be.

A glance at the temperature of Arctic animals, as given below, will show how little the temperature of the body in such animals differs from that of animals in temperate regions, though the difference in the temperature of the former, as compared with that of the surrounding atmosphere, may amount to as much as 76.7° C. (170° F.).

TEMPERATURE OF ARCTIC ANIMALS.[1]

Animal.	Temp. of animal.	Temp. of air.	Difference.
Arctic fox	41.5°C.(106.7°F.)	—25.6°C.	67.1°C.
" "	38.5	—20 6	59.1
" "	37.8	—19.4	57.2
" "	38.5	—29.4	67.9
" "	37.6	—26.2	63.8
" "	36.6	—23.3	59.9
" "	37.6	—23.3	60.9
" "	40.3	—20.3	70.7
White hare	38.3	—29.4	67.7
Fox	37.8	—26.2	64.0
"	41.1	—35.6	76.7
"	39.4	—32.8	72.2
"	38.9	—31.7	70.6
"	38.3	—35.6	73.9
Wolf	40.5	—32.8	73.3

On account of water being a better conductor, and having also a greater capacity for heat than air, the temperature of the body will fall more rapidly if exposed to cold water than to air at the same temperature; hence the great effect of cold baths in the treatment of fevers so much in vogue, particularly in Germany, in late years, and the great benefit derived from the application of ice in the treatment of sunstroke. While man and animals can resist the most intense Arctic cold by the agencies just referred to, nevertheless a far less degree of cold, if suddenly and directly applied to

[1] Gavarret, op. cit., p. 101. Parry's Journal, p. 130. Philadelphia, 1821.

the body, will soon prove fatal. Thus, according to Rosenthal,[1] animals die if the temperature of their bodies be reduced to 24° C. (75.2° F.), and such is usually the case in man also, as shown by the clinical cases referred to by the same high authority; though, as well known, the temperature in cholera may fall as low as 18.3° C. (64.9° F.). There are some other conditions in addition to those already mentioned which may affect the temperature of the body. Of such are the effects exerted by race, country, labor, sea-sickness, and barometrical variations. As such influences are, however, either exceptional or temporary in their character, we will not dwell further upon them, merely mentioning that, according to the late distinguished Professor Dunglison,[2] the temperature of the uterus during labor may rise as high as 41.1° C. (106° F.), that of the vagina at the same time being 40.5° C. (105° F.).

Production of Animal Heat.

Having considered the temperature of the body, and the various modifying conditions, it now remains to account for the production of this heat, and the manner in which the latter is regulated. Notwithstanding that a certain amount of heat is produced through the double decompositions and hydrations continually taking place in the economy,[3] there can be no doubt that, by far the greatest amount of heat produced is due, as Lavoisier supposed, to the slow combustion continually going on within the body of the animal, caused by the absorption of oxygen, the interchanging of which with carbon dioxide, etc., we have seen, constitutes the essence of respiration.

In the paper on the calcination of metals, brought before the Academy of Sciences, in 1775, Lavoisier[4] had shown that in the decomposition of mercuric oxide by heat the principle (oxygen) so obtained supported both combustion and respiration, whereas, when the same substance was reduced by carbon the principle then obtained (carbon dioxide) supported neither. These fundamental facts having been established, two years later Lavoisier[5] further showed that animals absorb oxygen and exhale carbon dioxide, and during the same year formulated a view on combustion in general in which respiration was regarded as a slow process of combustion, oxygen being absorbed and carbon dioxide and heat given off just as in the burning of coal. As might have been expected from the methods of investigation so characteristic of the great chemist and physiologist, Lavoisier soon instituted a series of experiments with the view of ascertaining whether the amount of carbon dioxide exhaled and heat produced by an animal in a given time was such as ought to be expected on the supposition that a certain amount of carbon had been burned in the body of the animal, the amount of

[1] Op. cit., s. 133. [2] Physiology, 1856, 8th ed., Vol. i., p. 602.
[3] D'Arsonval, Comptes Rendus, Aout 25th, 1879.
[4] Mem. de l'Acad. des Sciences, 1775, p. 520. [5] Ebenda, 1777, p. 183.

carbon dioxide given off and heat produced by the combustion of a similar amount of carbon outside of the body having been previously determined, and of so establishing the truth of his theory by experimental demonstration. For this purpose, in conjunction with Laplace, he invented the ice calorimeter.[1] This consisted essentially of three chambers, concentrically disposed; in the innermost chamber was placed the substance whose heat was to be determined, in the middle one ice, the melting of which was the measure of the heat produced, it having been previously determined how much heat is required to melt a given quantity of ice, while in the outer chamber ice was also placed in order to shield that in the middle chamber from the external temperature, the melted ice passing out by openings in the two outer chambers provided with stopcocks. Having determined by their experiments the amount of heat that would be produced by the burning of a pound of carbon Lavoisier and Laplace then placed a guinea-pig in the innermost chamber of their ice calorimeter, so modified as to permit of the free passage of a current of air, so that the respiration of the animal should not be interfered with, and found that the amount of carbon burned by the guinea-pig while in the calorimeter as deduced from the carbon dioxide expired was only sufficient to account for about nine-tenths of the heat produced as measured by the ice melted.

This fact, together with another one observed at the time, namely, that all the oxygen absorbed did not return in the carbon dioxide exhaled, led Lavoisier[2] afterward (1785) to the conclusion that of the oxygen inspired part combined with hydrogen to form water and that the heat developed by the combustion of the hydrogen, if added to that due to the combustion of the carbon, would account for the heat produced by an animal, as in the experiment with the guinea-pig, just described, and which could not be accounted for by the combustion of the carbon alone. The final conclusion of Lavoisier as to the nature of respiration and calorification, based upon the closest reasoning, observation, and experiments, extending over many years, is best expressed in his own words:[3] "Respiration is only a slow combustion of carbon and hydrogen, and which resembles in every respect that which goes on in a lighted lamp or candle, and, from this point of view, animals which respire are true combustibles, which form and consume themselves. In respiration, as in combustion, it is the atmospheric air which furnishes the oxygen and caloric,[4] but, as in respiration, it is the substance itself of the animal; it is the blood which furnishes the combustible. If animals do not repair habitually by food that which they lose in

[1] Mem. de l'Acad. des Sciences, 1780, p. 355.
[2] Hist. de la Societé Royale de Médecine, 1787, 568.
[3] Mem. de l'Acad. des Sciences, 1789, p. 570.
[4] To appreciate this passage it must be borne in mind that at the date when it was written oxygen was supposed to be composed of oxygen united with caloric, the principle of heat or fire, and that during the formation of carbon dioxide through the combination of oxygen with carbon the caloric was set free.

respiration, the oil will soon give out in the lamp, and the animal would perish, as a lamp extinguishes itself through want of feeding. The proof of this identity of effects between respiration and combustion is immediately furnished by experiment. In fact, the air which has maintained respiration does not contain any longer, at its exit from the lungs, the same quantity of oxygen; it contains not only carbonic acid [carbon dioxide], but, in addition, more water than it contained before inspiration."

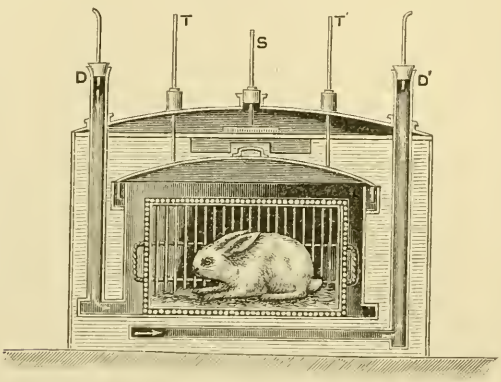
And now, after a lapse of more than a century, the only essential criticism that can be made upon the views of Lavoisier as to the origin of animal heat, apart from the hypothesis of caloric implied, is that he held that the lungs were the seat of the combustion, whereas it is known that combustion goes on in all parts of the body. But even while holding this view Lavoisier showed his profound appreciation of the nature of the phenomena, since he distinctly states, in one of his communications,[1] that possibly the carbon dioxide is not produced, but only exchanged with oxygen in the lungs. However important his generalizations, as to the matter of respiration and animal heat, nevertheless, dying on the scaffold a victim to the fury of the French Revolution, Lavoisier left his work unfinished. With the view of settling, if possible, some of the questions left undetermined by their great chemist, the Paris Academy offered, in 1821, a prize for the best essay on the origin of animal heat. The prize being awarded to Depretz, his essay was shortly afterward published,[2] that of the unsuccessful competitor, Dulong,[3] not, however, until several years afterward—in fact, after the death of its author. To avoid repetition, we will consider the calorimeters made use of by these experiments and the results obtained with them together.

The calorimeter of Dulong and Depretz did not differ in principle essentially from the water calorimeter previously made use of, for the same purpose, by Crawford.[4] It consisted essentially, like the latter, of two chambers, an inner one, in which the animal within a willow cage was placed, and an outer one, containing the distilled water, the elevation of whose temperature was taken as the measure of the heat produced by the animal. In the calorimeter of Crawford, however, while the air of the inner chamber was gradually diminished, and at the end of the experiment was transferred to an eudiometer for analysis, in that of Dulong and Depretz the air in the inner chamber was continually renewed by air from a gasometer, and being transmitted from the inner chamber through a spiral tube placed within the water of the outer chamber, passed thence into a water gasometer, where it could be measured and analyzed, the air, in the meantime, as it passed through the spiral tube, giving off the heat (communicated by the

[1] Mem. de l'Acad. des Sciences, 1777, p. 191.
[2] Ann. de Chimie et de Physique, 1824, Tome xxvi., p. 337.
[3] Ibid., 3ieme serie, 1841, Tome i., p. 440.
[4] Experiments and Observations on Animal Heat. London, 1788, p. 315.

animal) to the surrounding water, and so elevating its temperature. The amount of heat produced by the animal, as determined by the elevation of the temperature of the water, is expressed in calories, or heat units, a heat unit being the amount of heat necessary to elevate the temperature of a pound of distilled water one degree Cent. or Fahr., according to the thermometer used, or, as is more usually understood at the present day, the amount of heat necessary to elevate the temperature of one kilo. (2.2 lbs.) one degree Cent. The amount of heat produced by the animal expressed in heat units while in the calorimeter is then obtained by multiplying the weight of the water by the number of degrees by which the temperature of the water has been increased. Suppose, for example, that the water in the calorimeter weighed 20 kilo., and its temperature had been elevated as shown by the thermometers two degrees Cent., then 40 calories, or heat units, would have been produced during

Fig. 210.



Water calorimeter of Dulong.

the experiment by the animal, the latter having neither gained nor lost heat, since, if the animal gained heat, it is evident that all of the heat produced was not given off to the water, and if it lost heat the latter was not produced during the experiment, but simply radiated away from it, as would have been the case with any heated body. In the first case, the heat retained by the animal must be added to the heat as determined by the calorimeter; and, in the second case, the heat lost by the animal must be subtracted. In making calorimetrical experiments, therefore, the temperature of the animal must be taken at the beginning and the end of the experiment. It must be also remembered, however, that the materials entering into the composition of the calorimeter, such as copper, iron, brass, etc., absorb heat, even if in less amount than the water, and this heat also expressed in heat units must be added to that absorbed by the water. This can be readily estimated, the weight of the materials and their specific heat, or capacity for heat, being

known, the capacity for heat of water being taken as unity. Suppose, for simplicity, that the calorimeter is made out of copper, and that it weighs 10 kilo.; now the specific heat of copper being 0.09 that of water, it is evident that if the 10 kilo. of copper be multiplied by 0.09, the product 0.90, or the water equivalent, when multiplied by the two degrees Cent. equals 1.8, which will be the amount of heat expressed in heat units absorbed by the copper, and which must be added to the 40 heat units already obtained; or, what is the same thing, if the water equivalent of the copper 0.9, be added to the 20 kilo. of water, and the result 20.9 be multiplied by 2, the quotient will be the same as before—that is, 41.8 heat units produced by the animal. In other words, each kilo. of copper, having 0.09 the capacity of heat of a kilo. of water, 10 kilo. of copper may be regarded as equivalent to 0.9 kilo. of water, which, when added to the 20 kilo. of water and multiplied by 2, or the temperature gained, gives 41.8 heat units. It is hardly necessary to add, after what has just been said, that of the other metals usually entering into the construction of the calorimeter the heat absorbed by them, as well as that retained or given off by the animal, which, as we have seen, must be added to or subtracted from the 41.8 heat units, for example, according as the animal has gained or lost heat during the experiment, is determined in exactly the same way as in the case of the copper. As regards obtaining the water equivalent of the animal placed in the calorimeter—that is, its weight multiplied by its specific heat—a difficulty presents itself, since the specific heat of animals has not been absolutely determined. The latter is usually accepted as being 0.8,[1] that being the mean specific heat of the tissues so far determined, water being taken as unity. In determining the amount of heat given off by an animal in a calorimeter there is another consideration which must not be overlooked, and which is a slight source of error even in the best constructed calorimeters. That is the slight loss of heat due to conduction and radiation from the instrument, and which cannot be entirely prevented. The loss of heat from this cause, however, can be reduced to a very small amount by proper precautions, such as surrounding the calorimeter with down, etc., as was done by Crawford, or by lowering the temperature of the water in the calorimeter some degrees below that of the surrounding atmosphere, the supposition being that the heat absorbed from the surrounding air during the first half of the experiment would be radiated back again during the latter half, and that this source of error could, therefore, be neglected, as was admitted in the experiments of Dulong and Depretz. The loss of heat due to radiation, etc., can be also determined experimentally, and can be then taken into account in the final calculation; or, by self-regulating gas-jets, heat can be sup-

[1] Liebermeister, Handbuch der Pathologie u. Therapie des Fiebers, p. 147. Leipzig, 1875. Rosenthal, Archiv f. Anat., etc., 1878, p. 215.

plied to restore that which is lost. Further, it is important that the heat should be thoroughly diffused through the water in the calorimeter; this can be accomplished by the stirrers, as in the apparatus of Dulong and Depretz, or by any other suitable mechanical arrangement. The great improvement in the experiments of Dulong and Depretz, however, as compared with those of their predecessors, consisted in comparing the expired air with the inspired air, and determining the amount of heat produced and carbon dioxide exhaled simultaneously; whereas, in the experiments of both Lavoisier and Crawford, this was done with the same animal, but at different times. Notwithstanding the great number of experiments performed by Dulong and Depretz, and the general acceptance with which their views were received, not much importance can be attached to them at the present day on account of the following reasons: First. That the temperature of the animal within the calorimeter was assumed to remain unchanged during the experiment, although Lavoisier had distinctly called attention to the improbability of such being the case. Second. Of the amount of carbon dioxide exhaled by the animal being underestimated, part of it being absorbed by the water of the gasometer into which it passes. Third. Of the amount of heat, as deduced from the carbon dioxide exhaled, being also underestimated, both on account of the estimate of Lavoisier of the heat produced by the combustion of carbon and hydrogen obtained with an ice calorimeter, being accepted as the basis of comparison with the heat produced by an animal in a water calorimeter, and because the heat-producing power of the carbon and hydrogen burned even, as determined by Lavoisier, is manifestly too low as shown by the later and accurate experiments of Fabre and Silberman;[1] and further, that no account was taken of the heat produced by the burning of the sulphur and phosphorus in the animal economy. Fourth. That the ratio of the carbon to the hydrogen was erroneously estimated, an important source of error, since far more heat is produced by the combustion of hydrogen than by an equal weight of carbon. Fifth. From the carbon and hydrogen, to whose combustion is the heat principally due, being supposed to exist in the free condition, which they evidently do not.

Later investigators have endeavored to utilize the results of Dulong and Depretz in considering them as influenced by the conditions just referred to, but as the attempts have been far from satisfactory, it is not necessary to dwell upon them.

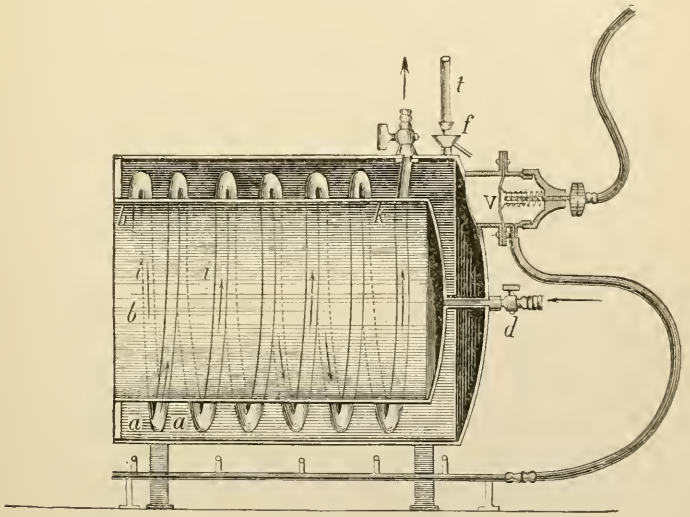
During late years a number of investigations have been made calorimetrically, with the object of determining the heat produced by an animal in a given time. Among these may be mentioned especially those of Senator[2] upon dogs. The calorimeter used in these experiments was essentially the same as that of Dulong's, the

[1] Ann. de Chimie et de Physique, 3ieme ser., Tome xxxiv., p. 357; Tome xxxvi., p. 51; Tome xxxvii., p. 405.

[2] Archiv f. Anat. u. Phys., 1872, s. 1, 1874, s. 18.

only difference being that it was usually filled with warm water in order to prevent the animal losing heat. The ventilation of the chamber in which the animal was placed was maintained by aspiration, the current of air, before entering the calorimeter, being freed from its carbon dioxide by passing it through potash, and the carbon dioxide exhaled into it by the animal being determined after it left it by Pettenkofer's method. In the final estimation of the heat produced by the animal, in addition to that taken up by the calorimeter, the heat absorbed by the air passing through the instrument was also considered. Senator found, as the mean of his experiments, that a dog fed daily produced 16.5 calories or heat units per hour, with an exhalation during the same time of 4.4 grammes of carbon dioxide, there being produced, as a general rule, 2.5 calories for every kilogramme (2.2 pounds) of weight. In order to obtain the amount of heat produced in twenty-four hours, the 16.5 calories were multiplied by 24, but as it is uncertain whether the production of heat is constant, this is hardly admissible. The general conclusion to be drawn from the experiments of Senator is, that there is no constant relation existing between the production of heat and the exhalation of carbon dioxide, and while during digestion the production of both is increased, in starvation both are diminished.

Fig. 211.



Calorimeter.

The calorimeter (Fig. 211) made use of by the author consists of two copper cylinders concentrically disposed, the outer space *a* or the space between the cylinders being closed at both ends with copper, the inner space *b*, or the space within the cylinder, being closed at one end by copper, and at the other end by an annular door consist-

ing of brass and glass, and which can be hermetically closed by the brass clamps and rubber facing soldered to the brass rim internally. The outer chamber *a* is filled with distilled water by means of a funnel introduced through the opening *f*, and when full contains 18.1 kilo. (40 lbs.) of water. The inner chamber *b*, at the end opposite the door, communicates by a stopcock (*d*) with the external air, and through the opening *h* in its roof with a copper spiral, which, after making a dozen turns around the inner cylinder within the water of the outer chamber, terminates in the opening *k* of the latter. By means of the mercurial pump (already described) the ventilation of the inner chamber can be thoroughly maintained, the air entering the latter through the opening at *d* and passing thence by the opening *h* into the spiral *i* and out by the opening *k* with the same temperature at which it entered, the heated air being gradually cooled as it passes through the spiral, the heat being absorbed by the surrounding water. If it is desired to compare the expired with the inspired air, the air freed from its water and carbon by Voit's method is made to pass through a meter, before it enters the calorimeter and through one after it leaves it, being previously freed from its water and carbon in the same manner as was the inspired air. Fitting in the floor of the inner chamber of the calorimeter is a movable copper pan with a sieve-like cover on which the animal rests, the object of the cover being that the urine of the animal can trickle into the pan and insure cleanliness. Ventilation having been assured by the action of the pump and the temperature of the water in the outer chamber noted by introducing a thermometer into the opening *f* and that of the animal taken, the latter, having been previously weighed, is placed within the chamber on the tray and the door securely closed. Suppose the experiment has lasted one hour, and it be admitted that the heat lost by radiation and conduction from the calorimeter be replaced by that furnished by the gas jets,[1] the flow of gas being regulated by the valve V, which with the heating of the water is pressed outward (through the pressure of the column of water in the tube *t*, replacing the thermometer) against the opening transmitting the gas and thereby diminishing its flow, and which with the cooling of the water, is drawn back again from the opening, thereby increasing it again. To determine the calories or heat units produced by the animal, a rabbit, for example, during the time mentioned, we have only now to multiply the number of degrees by which the temperature of the water has been increased by its weight, to which has been added the water equivalent of the copper, brass, glass, rubber, and solder entering into the construction of the calorimeter, and adding or subtracting the heat gained or lost by the animal as determined immediately at the conclusion of the experiment. Suppose that the temperature of the water in the calorimeter has increased 0.5° C., the temperature

[1] By enveloping the calorimeter with a thick jacket of wool or feathers the gas jets can be dispensed with.

at the beginning of the experiment being 15° C. (59° F.), and at the end 15.5° C. (59.9° F.), and the

Water equivalent,	copper	=	21 lbs.	×	0.095	=	1.995
"	brass	=	23.25 lbs.	×	0.093	=	2.162
"	iron	=	0.09 "	×	0.11	=	0.009
"	glass	=	1.25 "	×	0.19	=	0.237
"	rubber	=	0.6 "	×		=	0.0[1]
"	tin	=	0.5 "	×	0.05	=	0.025
"	lead	=	0.5 "	×	0.03	=	0.015
"	materials					=	4.443

Adding the water equivalent of the materials used, 4.4 lbs., to the weight of the water, 40 lbs., making 44.4 lbs., or 20.1 kilo., and multiplying the latter by 0.5° C., the number of degrees gained by the water, the product, 10.05, will be the number of calories or heat units produced by the animal, supposing the temperature of the latter to have remained unchanged. Suppose the animal, however, lost 0.9° C., its temperature being 39.2° C. at the beginning of the experiment and 38.3° C. at the end, then there must be subtracted from the 10.05 calories 2.16—that is, the product of the weight of the rabbit, 6.6 lbs., or 3 kilo., by its specific heat, 0.8° by 0.9° ($3 \times 0.8 \times 0.9 = 2.16$); the total number of heat units produced by the rabbit in an hour would then be 7.8 calories. If the rabbit gains the same number of degrees, then the 2.16 calories must be added to instead of being subtracted from the 10.05 heat units, making the total amount of heat produced 12.21 heat units.

In the experiment just described it was assumed that the temperature and aqueous vapor of the air issuing from the calorimeter was the same as that entering it. If, however, the air, as it passes through the calorimeter, and the water evaporated from the lungs and skin, absorb heat the amount of heat so expended being also produced by the animal, as well as that imparted to the water of the calorimeter, must be determined and added to the latter. The amount of heat absorbed by the air passing through the calorimeter is readily obtained by reducing the given volume of air to that of standard pressure and temperature and multiplying the weight of the latter, first by its specific heat, 0.26, and then by the number of degrees by which its temperature is increased. The heat expended by the animal in evaporating the water from its lungs and skin is estimated by determining first the difference in the amount of the water of the air passing in and out of the calorimeter, and multiplying the weight of the excess of the water by 582, that being the number of heat units expended in evaporating 1 kilogramme of water.

It should be mentioned in this connection that a small amount of heat is carried off in the urine and feces voided by the animal

[1] The specific heat of rubber slip not having being determined, the heat actually produced was slightly greater than that given in text. The amount, however, would be so small that it may be neglected.

which is usually neglected in calorimetrical experiments. We shall see, however, that in estimating the total amount of heat produced by the animal that the heat so dissipated though small in amount must be taken into consideration.

Calorimetrical investigations have been made also upon man by Scharling,[1] Vogel,[2] and Hirn,[3] but with rather unsatisfactory results. The apparatus made use of by these experimenters was essentially the same, consisting of a chamber in which the man was placed and which was kept in a room maintained at a temperature as constant as possible, the increase in the temperature of the chamber, together with the heat lost through cooling, being regarded as produced by the man during the experiment. Since the temperature of the chamber after being somewhat elevated after that remains constant, the heat as produced being radiated away, according to the Newtonian law of cooling, the amount of heat produced will be equal to the difference between the constant temperature and the initial temperature multiplied by the coefficient of cooling, the latter being determined experimentally. In the experiments of Scharling and Vogel this was accomplished by placing a vessel filled with hot water in the chamber and comparing the loss of heat of the water with the increase of the temperature of the chamber, and in those of Hirn by burning hydrogen and comparing the actual result with that obtained by calculation. On account of the many sources of error incidental to such a crude method of experimentation as that just described, an approximate value only can be attached to the results so obtained, and the same may be said of the estimates of the amount of heat produced based upon the rise in the temperature of the water of a bath in which a man is immersed,[4] or of that of a calorimeter inclosing only a part of a person, a limb, for example.[5] Nevertheless, it should be mentioned that the estimates of these observers of the heat produced by a man in twenty-four hours do not differ as much as might be supposed, amounting, according to Scharling, Vogel, Hirn, Liebermann, and Leyden, to 3168, 2400, 3720, 3525, and 2376 calories respectively, allowance being made for the size and weight of the individual experimented upon.

Since the heat produced by an animal is due to the combustion of its food it might be supposed that it would be only necessary to determine the amount of carbon, hydrogen, sulphur, phosphorus, etc., that it contained, and the products of their combustion, carbon dioxide, water, urea, etc., obtained from the excreta in order to determine the amount of heat produced. It must be borne in mind, however, that to effect the combustion of the food—that is, to

[1] Journal für pract. Chemie, xlviii., s. 435, 1849.

[2] Archiv d. ver. f. Wiss. Heilk. Neue folge, Band i., s. 441, 1865.

[3] Recherches sur l'equivalent mécanique de la chaleur, Colmar, 1858. Exposition analytique et experimentale de la theorie mecanique de la chaleur, 3d ed., T. i., p. 27. Paris, 1875.

[4] Liebermeister, op. cit., p. 239.

[5] Leyden, Deutsch. Archiv f. klin. med., 1869, s. 273.

transform it into carbon dioxide, water, etc., a certain amount of heat, or an equal amount of energy of some kind, is required, since the carbon, hydrogen, and other combustible matters do not exist in the food in the free gaseous state, but in a state of molecular combination. A certain unknown amount of heat would have to be deducted therefore from the amount estimated if based upon an analysis of the food and the excreta. In other words, the heat producing power of food, or any fuel, cannot be estimated from the amount of combustible matters it may contain, since the heat to be expended in breaking up the chemical combinations constituting these matters, and of setting free the heat previously locked up in them is practically unknown. It is for the reasons just given, as well as for the further one of the accepted estimates of Dulong of the amount of heat produced by the combustion of a given weight of carbon, hydrogen being too low, that the calculation of Helmholtz[1] of the amount of heat produced by a man weighing 82 kilo. in twenty-four hours, viz.: 2731.2 calories, can only be accepted as approximating the truth. And while the calculation of Ludwig,[2] of a daily production on the average of 3191.9 calories is free from the last source of error mentioned, being based upon the data of Barral and the higher estimates of Fabre and Silberman of the heat value of the carbon and hydrogen burned, nevertheless, as it also assumes that the combustion of the carbon and hydrogen of the food develops as much heat as if existing in the free condition, it is open to the same objection as the calculation of Helmholtz. In fact, the only way in which the amount of heat produced through the combustion of food can be actually determined, is by burning it in a calorimeter, as was done by Frankland,[3] and of so obtaining its heat value by direct experimentation. The instrument we make use of for this purpose, the same as that of Frankland, of the convenient form devised by Thompson, consists of a copper cylinder with a capacity of 120 c. cm., open below, and with the rim perforated with small openings, but closed above, and with the cavity of the cylinder prolonged into a narrow tube provided with a stopcock near its end, and of a smaller cylinder with a capacity of 15 c. cm., open above, but closed below, the lower portion of the cylinder fitting into the little cup of the stand, the latter being provided with three elastic springs which securely hold the large cylinder when the latter encloses the small one. Within the small cylinder is placed the substance to be burned with a small fuse attached with a combustible whose heat values are known. The latter being lighted, the large cylinder is immediately placed over the small one, the elastic springs holding it fast, and the instrument so put together at once plunged into a long, narrow vase containing a known quantity of distilled water whose temperature

[1] Encyl. Wörterbuch der Med. Wissen., Band xxxv., s. 555. Berlin, 1846.
[2] Lehrbuch der Physiologie des Menschen, Zweiter Auflage, Zweite Band, s. 749. Leipzig, 1861.
[3] Philos. Mag., 1866, xxxii., p. 182.

has been accurately determined by a specially constructed thermometer graduated into tenths. In a few moments fumes will be seen to issue from the holes in the rim of the outer cylinder into the surrounding water. The deflagration being ended, and the stopcock opened, the water will rise through the holes into the cylinders. The instrument being moved up and down, the heat given out will soon diffuse itself equally throughout the water, the amount of heat produced by the food burned being determined by the elevation of the temperature of the latter, due allowance being made on the one hand for the heat absorbed by the copper, etc., and on the other for that produced by the burning of the fuse and combustible used. The other sources of error incidental to the working of the apparatus are so slight that they may be, according to Frankland, neglected. It was by means of the calorimeter just described that Frankland determined by actual experiment the amount of heat developed by the combustion of different kinds of food.

HEAT DEVELOPED BY BURNING 1 GRAMME (15.4 GR.) OF DIFFERENT ARTICLES OF FOOD EXPRESSED IN HEAT UNITS.[1]

A heat unit is equal to the amount of heat necessary to raise the temperature of 1 kilo. (2.2 lbs.) of distilled water 1° C. (1.8° F.).

	When oxidized outside of body.		When oxidized inside of body.	
	Dry.	Natural condition.	Dry.	Natural condition.
Cod-liver oil	. . .	9.107	. . .	9.107
Fat of beef	9.069	. . .	9.069	. . .
Butter	. . .	7.264	. . .	7.264
Guiness' stout	6.401	1.076	6.401	1.076
Arrowroot	. . .	3.912	. . .	3.912
Lump sugar	. . .	3.348	. . .	3.348
Grape sugar	. . .	3.227	. . .	3.227
Yelk of egg	6.460	3.423	6.24	3.30
Hard boiled egg	6.321	2.383	6.05	2.28
Cheese	6.114	4.647	5.74	4.36
Mackerel	6.064	1.789	5.71	1.61
Lean of beef	5.313	1.567	4.85	1.42
Milk	5.093	0.662	5.07	0.62
White of egg	4.896	0.671	4.21	0.57
Veal	4.514	1.314	4.02	1.11
Ham (boiled)	4.343	1.980	3.68	1.68
Bread (crumb)	3.984	2.231	3.84	1.45
Flour	. . .	3.936	. . .	3.84
Rice (ground)	. . .	3.813	. . .	3.76
Cabbage	3.776	0.434	3.65	0.42
Potatoes	3.752	1.013	3.69	0.99

It will be seen, however, from a glance at the above résumé of Frankland's experiments, that the fatty and carbohydrate foods are as thoroughly burned in the body as out of it, though more slowly, whereas the albuminous substances are but imperfectly so. This is as might have been expected, since, as we have already mentioned, except in certain temporary conditions in

[1] Frankland, op. cit.

a state of health, fat and starch are never found in the excreta, these substances passing out of the body as carbon dioxide and water, being as thoroughly oxidized within the system as if burned in pure oxygen outside of it, whereas, as we shall presently see, uric acid and urea are normal constant ingredients of the excreta, these substances representing so much unburned proteid which passes out of the system in this form.

Thus, according to recent researches, while 1 gramme of muscle extracted with water will produce, when burned out of the body, 5.778 calories, the same amount of muscle will produce, when burned in the body, only 4.937 calories, the difference of 0.841 of a calorie being due to the fact that one-third of the proteid passes out of the economy unburned as urea, and that one-third of a gramme of urea will produce, when burned outside of the body, 0.841 of a calorie. In estimating the amount of heat produced by the burning of any proteid substance within the body one-third is usually deducted as representing so much incombustible material; for, although in all probability proteid is converted by combustion into carbon dioxide, water, and ammonia, as the latter combines with part of the carbon dioxide and water to form ammonium carbamate, the antecedent of urea; of the heat liberated by the combustion one-third is locked up again in the subsequent synthesis.

According to recent experiments, made with improved form of calorimeters, the different food stuffs when burned in the body will produce as follows:

Carbohydrates	4.116 calories.
Proteids	4.937 "
Fats	9.312 "

Having learned the amount of heat developed in the burning of a given weight of carbohydrate, proteid, and fat, etc., out of the body, it still remains, knowing by analysis how much of such substances is contained in the food, to determine from the carbon dioxide, water, and urea in the excreta, the products of the combustion of such substances, the amount actually burned in the body, and of so estimating, by means of the above data, the amount of heat developed within the body on a normal diet, or otherwise. In other words, the ingesta or the food must be compared with the egesta or the excretions. The subject of the observation must be weighed at the beginning and the end of the experiment to learn whether the weight has remained unchanged, since, if the individual loses weight, the food has been deficient, the body wasting to supply it; and, if the reverse is the case, the food has been in excess, the body fattening. Further, the experiment should extend over a period of twenty-four hours, and longer, when possible, in order to avoid the usual source of errors incidental to all experiments of such a character if lasting for shorter periods of time. It was on such principles that the admirable experiments of Ranke, performed upon

himself, were conducted, and it may be mentioned, incidentally, in this connection, that at that time the distinguished physiologist was twenty-four years old, six feet high, weighed one hundred and fifty-four pounds (70 kilo.), was in perfect health, and that the apparatus made use of was the Pettenkofer respiration apparatus that we have already referred to. The results obtained by Ranke[1] are shown in the following table:

HEAT PRODUCED IN 24 HOURS BY THE COMBUSTION OF FOOD WITHIN THE BODY AS ESTIMATED FROM THE EGESTA, AND EXPRESSED IN HEAT UNITS.

Nitrogenous Diet.

Ingesta.		N	C	Egesta.		N	C
Meat,	1832 grammes.	62.29	229.36	Urea,	86.3	40.28	17.26
	1300 " consumed,	44.19	162.75	Uric acid.	1.9	0.65	0.70
Fat of meat,	70 "	0.00	50.27				
Salts,	31 "	. . .	. . .	Salts,	26.6		
Water,	3371 c. c.	. . .	. . .	Urine,	2073 c. c.		
Fat of body,	75.14 grammes,	0.00	54.02	Feces,	99.0	3.26	14.88
Water "	71.00 "	. . .	. . .	Respiration,			231.20
		44.19	267.04			44.19	267.04

Initial weight . . . . 72.927 kilogrammes.
Terminal weight . . . . 72.781 "
0.146 gramme.

Heat units produced 2779.5

Starvation Diet.

Ingesta.		Egesta.	
Body consumed.		Urea,	18.3 grammes.
Albumin,	54.45 grammes.	Uric acid,	0.24 "
Fat,	195.94 "	Respiration,	180.00 cubic meters.

Heat units produced 2012.8

Non-nitrogenous Diet.

Ingesta.		Egesta.	
Starch,	300 grammes.	Urea,	17.1
Sugar.	100 "	Uric acid,	0.54
Fat,	150 "	Feces.	90.00
Albumin of body.	51.55 "	Respiration,	200.00 cubic meters.

Heat units produced 2059.5

Mixed Diet.

Heat units produced 2200

It will be observed from the above that the greatest amount of heat was produced on a nitrogenous, or a very abundant meat diet, but that this was accomplished at the expense of the body, Ranke losing 146 grammes in weight, his body supplying 75.14 grammes of fat in addition to the 70 grammes of roast meat and 71 grammes of water, and that of the 1832 grammes of meat eaten only 1300 grammes were burned, as shown by the amount of urea excreted. It follows, therefore, that, so far as the production of heat was concerned, the same result might have been obtained

[1] Ranke, Physiologie, Dritte Aufl., s. 196, s. 566. Leipzig, 1875.

with 532 less grammes of meat, but with 71 more grammes of fat. On the other hand, as Ranke mentions in speaking of the heat produced on a non-nitrogenous diet, of the 150 grammes of fat eaten only 68.5 grammes could have been burned, 81.5 grammes having been deposited in the body. On such a diet, therefore, more than half the fat, if taken with the view of producing heat, would be superfluous.

The amount of heat produced upon a mixed diet such as that of Ranke's, as determined from an analysis of the excreta, is somewhat less than that obtained by multiplying the different amounts of food stuffs contained in such a diet by the number of heat units — we have supposed each gramme of the same would produce when burned in the body, as may be seen from the following calculation :

Carbohydrates	240 grammes	× 4.116 =	987.84	calories.
Proteids	100 "	× 4.937 =	493.70	"
Fats	100 "	× 9.312 =	838.08	"
Total	340	=	2319.62	

The difference amounting to about one hundred calories can be to a great extent accounted for, however, when it is remembered that Ranke assumed that one gramme of proteid, when burned in the body, would produce 4.263 instead of 4.937 calories. That the two methods of investigation when properly applied to the same animal will give almost identical results was shown by Rubner,[1] by an experiment made with a dog in which the heat produced by the animal as determined directly by the calorimeter differed from that as determined indirectly by analysis of the excreta by less than 0.5 per cent. While the heat produced upon a mixed diet was regarded by Ranke,[2] Vierordt,[3] and Voit,[4] respectively, as amounting to 2200, 2497, and 3066 calories, according to the more recent investigations of Danilewsky,[5] 3210 calories are produced upon a mixed diet, moderate work being done and as much as 3780 calories, the work being of a very laborious character. Let us assume, however, with Ranke that the heat liberated by the burning of the food amounts to only 2200 calories, that is, will elevate the temperature of 2200 kilo. of water 1° C. or 70 kilo. 31.4° C. (154 pounds 56.5° F.). Such an amount of heat if applied to the heating of a human body weighing 70 kilo. would elevate the temperature 34.1° C. (61.3° F.), or 2.7° C. (4.8° F.) higher, since a human body consisting of only three-fifths water, 42 kilo., and two-fifths tissue, 28 kilo., and the latter having a specific heat, 0.8 that of the water, the 2200 heat units would be applied to heating the equivalent of 64.4 kilo. (146 pounds) of water, instead of 70 kilo. (154 pounds) (28 × 0.8 = 22.4 water

[1] Zeitschrift für Biologie, Band 30, 1893, s. 136.
[2] Op. cit., s. 207. [3] Physiologie, Vierte Aufl., 1871, s. 257.
[4] Hermann, Handbuch, Sechster Band, s. 525.
[5] Pflüger's Archiv, Band 30, 1883, s. 190.

equivalent, $22.4 + 42 = 64.4$, $\frac{2200}{64.4} = 34.1°$). In other words the tissue of the human body, from this point of view, bears the same relation to its water as the brass, copper, etc., do to the water of the calorimeter, the human body, in fact, serving as a calorimeter for the determination of the heat produced by foods when burned within the body. If, however, the heat produced upon a mixed diet will elevate the temperature of a human being weighing 70 kilo. 34° C. in 24 hours, then at the end of that time the temperature of such a person should be about 70° C. (126° F.), and at the end of 48 hours 104° C. (219° F.), instead of 36° C. (98.9° F.), the normal temperature; as a matter of fact, however, we have seen that the temperature of the human body varies but little.

It now remains for us, in conclusion, to endeavor to account for this constant temperature somewhat more in detail than we have already done, and that leads us to the consideration of how the heat produced is expended.

Expenditure and Regulation of the Production of Heat.

We have seen that there are produced within the human body in twenty-four hours at least 2300 calories, or heat units; that is, heat enough to raise the temperature of 2300 kilo. of water 1° C., or 23 kilo. 100° C., or from the freezing to the boiling point. It is very evident, therefore, that were such a production of heat kept up, and the heat developed not dissipated, but retained in the body, that the latter in the course of two days, would boil. A little reflection will show, however, that, in addition to the heat given off through radiation and conduction, if the temperature of the body be higher than that of its surroundings, that a certain amount of heat leaves the body in a latent condition, so to speak, locked up in the watery vapor exhaled from the lungs and skin, and from the fact of the solid and liquid food, and the air breathed entering the body at a lower temperature, 15° C. (99° F.), for example, than that of the latter, and leaving it at the same temperature, 37.1° C. (98.9° F.), heat must also be absorbed, and that there must be a still further expenditure of heat in the accomplishing of bodily and mental work, since there can be no doubt that, whatever be the nature of muscular and mental energy, the latter is correlated in some way with heat, the disappearance of the one being coincident with the appearance of the other. Now, from the very nature of the case, the relative amounts of heat expended in the ways mentioned must vary very much, according to the character of the climate, of the quantity and quality of air breathed, of food taken, of the amount of muscular and mental work performed. It is therefore impossible, if for these reasons only, to indicate exactly what becomes of the heat developed in the body. Further, too much importance must not be attached to any tabular résumé of the

expenditure of heat, since the data upon which such a résumé must be based are, to a certain extent, assumed. It is only offered as illustrating in a more detailed way the general observations regarding the expenditure of the heat just made, and as also showing the manner in which a table could be drawn up if all the data had been without cavil experimentally determined. It should be mentioned, however, that this criticism applies only to the relative amounts of expenditure of the heat, the total amount of heat leaving the body being, of course, that produced if the temperature of the body remains constant.

We will suppose that the food of a man weighing 70 kilo. (154 pounds) produces in twenty-four hours 2300 calories, or heat units; that the food of such a man, including the air breathed, be known; that the specific heat of the food be accepted as being 0.8, and that of the air 0.26; that the amount of watery vapor exhaled from the lungs and skin has been determined; that it be admitted that it requires 582 heat units to vaporize 1 kilo. of water and that the muscular work performed by the man during a day be considered as amounting to 112397 kilogrammeters, that is to say the man lifts 112397 kilo. through one meter (358 tons through one foot), and that the amount of heat necessary to raise the temperature of one kilo. of water 1° C. or a heat unit if applied mechanically would lift 423 kilo. through one meter (1.3 tons through one foot), then according to the above data the heat produced will be expended somewhat as follows:

EXPENDITURE OF HEAT.

1.5 kil. (3.3 lbs.) water . . .	34.5 heat units.	1.50 per cent.
1.5 " solid food, raised 23° C. (73°F.)	27.6 " "	1.20 " "
16.0 " (35.2 lbs.) air inspired . .	95.6 " "	4.15 " "
19.0 kil. (41.8 lbs.)	157.7 " "	6.85 " "
0.4 kil. (0.8 lbs.) water ev. from lungs	232.8 " "	10.12 " "
0.6 " (1.32 lbs.) " " " skin	384.1 " "	16.70 " "
1.0 kil. (2.2 lbs.)	616.9 " "	26.82 " "
Radiation and conduction . .	1272.6 " "	55.32 " "
External or muscular work . .	252.8 " "	10.99 " "
	2300.0 " "	100.00 " "

Ratio of muscular work to heat 1 to 9.

It will be observed, that of the 2300 heat units produced in twenty-four hours, about 7 per cent. are expended in warming the food, including the water and air breathed; 26 per cent. in evaporating the water from the lungs and skin; 55 per cent. in radiation and conduction from the general surface of the body, and about 11 per cent., or one-ninth, of the whole heat produced in the performance of external or muscular work. Of the 55 per cent. of heat that we have supposed is radiated or conducted away, part must be regarded as that heat which we have seen is expended mechanically in performing the internal work incidental to the circu-

lation and respiration, but which in being transmuted finally into heat again, leaves the body in that form rather than as mechanical energy. While no numerical estimate can be given, as yet, of the relation existing between heat and nervous energy, there can be no doubt, however, that the latter, like all other kinds of energy, must be developed out of some equivalent form, and leaves the body as such, or as some other mode of motion. That nervous energy is developed out of heat appears very probable from the experiments of Lombard, already referred to, and by which it was shown that, while all mental action was accompanied with the production of heat, that more heat disappeared during deep thought than during reading to one's self, for example, of emotional poetry; further, it was shown by the same experimenter that more heat disappeared than when the reading was aloud—that is, had a muscular expression, part of the heat produced in the latter case being applied to making the oral or muscular effort. It is a matter of daily observation that silent grief is deepest, that pent-up emotion finds relief in physical action. This is in accordance with the results of the experiments just mentioned, since the heat that is transformed into emotions or ideas, in the one case, becomes muscular action in the other, and just in proportion as there is more of the one, so there is less of the other. Hirn[1] endeavored to determine, experimentally, the exact quantity of heat expended in the performance of mechanical work by comparing the heat produced within a definite time with the work done, the latter consisting in a man raising his own weight through a given height, the man walking upon the circumference of a tread-wheel rotating in the opposite direction to himself. According to Hirn, a man weighing 75 kilo., during an hour's work upon the tread-wheel placed within the calorimeter, produced 430 heat units, whereas, judging from the amount of oxygen absorbed and carbon dioxide exhaled, 500 heat units were produced. What, then, became of the 70 extra heat units? According to Hirn, it was at the expense of this amount of heat that the 29,610 kilogrammeters of work were accomplished—that is, of raising 75 kilo. through nearly 400 meters

$$\left(423 \times 70 = \frac{29610}{75} = 394\right).$$

On account, however, of the errors incidental to the construction of the apparatus, and of the amount of heat produced as determined from the oxygen absorbed being estimated as too high, the results of Hirn, as just given, cannot be accepted; nevertheless, the difference between the amount of heat that appeared, as such, and that which ought to have appeared, can only be accounted for on the supposition that part of the heat produced was expended in the performance of mechanical work, and, as a corollary, it follows that less heat appears during a muscular contraction, when accom-

[1] Op. cit., Tome i., p. 35.

panied with work, than when without, and which accords with daily experience.

Having considered the manner in which animal heat is produced and expended, it remains for us now to account, so far as is possible, for the fact that the temperature of a hot-blood animal is maintained nearly constant, notwithstanding the variations in that of its surroundings. Among the conditions regulating the production of animal heat may be mentioned the taking of solid and liquid food, the character of the respiration and circulation, the action of the skin, the influence of bodily size.

While the amount of heat produced will depend on the quality and quantity of the food, the mere taking of the latter in the form of hot or cold drinks, for example, with the view of increasing or diminishing the general temperature of the body, as is so commonly done, will have, as already mentioned, but little effect. The effect of cold drinks in lowering the general temperature of the body must be also equally slight and temporary. On the other hand the effect of a hot drink, as we have seen, may be exactly opposite to what might have been expected, not only through the cooling effect due to the evaporation as in the drinking of hot tea, but on account of the specific substance of which the hot drink consists. Thus, for example, if hot spirits be taken, while at first a sense of warmth is experienced, with the paralysis of the vasomotor nerves by the alcohol, a greater quantity of blood flowing to the skin than usual, a proportionally larger quantity of heat will be lost from the general surface, and the effect of the hot drink will be in the long run, therefore, to lower the temperature of the body rather than to raise it. It has already been mentioned that about 4.1 per cent. of the heat produced is expended in warming the inspired air, and it might naturally be supposed that if the respiration be quickened and the amount of air inspired increased, that a proportionally greater quantity of heat would then be expended in warming it. Such would appear to be the case, dogs and other animals panting when overheated, since they sweat only in those parts destitute of fur or hair, and the cooling effect of the perspiration being absent, the excess of heat developed is carried away in the expired air. The respiration when quick, will be more efficient, therefore, in lowering the general temperature of the body than when slow. Hence, also, the rapidity of the breathing in heat dyspnœa, a condition due to the exposure of the body to a high temperature. Under such circumstances a considerable amount of heat is carried away in the expired air, and the temperature of the body is thereby prevented from rising as high as it would be without such compensatory influence. On account of so much heat being given off from the skin amounting through radiation, conduction, and evaporation, to nearly eighty per cent. of the heat produced, any change in the condition of the latter, as regards its structure or the amount of blood circulating through it, etc., will materially influence the general temperature of the body.

Were the temperature of the skin constant, the amount of heat given off or taken up by it would depend simply upon that of the surrounding atmosphere, the skin losing heat if the temperature of the air was lowered, and gaining heat when that of the air was elevated. As a matter of fact, however, when the body is exposed to a temperature cooler than its own, the vessels of the skin contracting, the general surface becomes cooler, the difference between the temperature of the body and the surrounding air being diminished, the loss of heat is correspondingly diminished; on the other hand, when the body is exposed to a higher temperature than its own, the vessels of the skin expanding, the general surface becomes warmer, and a correspondingly greater amount of heat is lost.

It is a cause frequently of surprise to most persons to learn that, no matter how hot or cold they may feel, the temperature of their body nevertheless remains practically the same. From what has just been said, however, as regards the action of the skin in regulating the temperature of the body, it is obvious that in the cooling of the body through the evaporation from the cutaneous surface, when exposed to a higher external temperature, the greater quantity of hot blood then circulating through the cutaneous vessels will, in impressing the sensory nerves, give rise to a general sense of warmth, so that while we feel warmer our body is actually getting cooler through the loss of heat involved in the evaporation. On the other hand, when, through the exposure to extreme cold, the cutaneous vessels are diminished in size, the smaller quantity of hot blood circulating through them will give rise to a sense of coolness, so that while we feel cool our body is actually becoming warmer through retention of the heat of the blood within it. The feeling warm or cold depends, then, simply upon the relative amounts of blood circulating in the skin.

The effect of the successive exposure of the body to cold and heat, as just described, is well seen in the taking of cold baths. While in the bath, the vessels of the skin being contracted, the latter is pale and cold, and the heat is retained, on emerging from the bath the vessels being dilated, the skin is red and warm, and heat is then given off from the surface. When we come to study the structure of the skin somewhat in detail, we shall see that its adipose tissue, being a bad conductor, prevents any great amount of heat from being given off from the inner parts of the body to the surface, and so lost.[1] This effect being especially well-marked in those cases where the difference in temperature on both sides of the skin does not amount to more than about 9° C. (16° F.), the significance of the good effect of wearing clothing becomes apparent, since under such circumstances the body of a man is surrounded by a layer of air having a temperature of about 30° C. (86° F.), the temperature under the skin being[2] 36° C. (96.8° F.), the difference

[1] Klug, Zeits. für Biologie, x., s. 73.

[2] Becquerel and Breschet, Ann. des Sciences Nat., 2ieme ser., Tome iii., p. 257; Tome iv., p. 243.

amounting, therefore, to only 6° C. (12.8° F.). Clothing in man plays the same part as hair, fur, and feathers in animals, the air inclosed within the latter, through being a bad conductor, practically prevents any great loss of heat from the general surface. Man, however, is far better able to adapt himself to changes in climate than most animals, since through change of clothing, food, etc., and free action of the skin, he is able to live in tropical or temperate regions as well as in arctic ones.

It has already been mentioned that through the evaporation of the water from the skin as sweat about sixteen per cent. of the heat produced is expended, and that the amount of water evaporated will depend, among other conditions, upon the amount of water already existing in the atmosphere. It is very evident, therefore, that the temperature that a person can endure must soon reach a limit, since if the temperature of the surrounding air keeps continually rising, and becomes saturated with watery vapor and is unchanged, the body, notwithstanding what has just been said of the action of the lungs, skin, etc., will become as hot as its surroundings. It is easier to keep out cold—that is, to keep in the bodily heat by proper food, clothing, and active exercise—than to keep out heat. Travellers, when properly fed and clothed, complain less of the cold of the arctic regions than of the heat of the tropics—indeed, it is said that while crossing the Red Sea, at certain seasons of the year, with all precautions taken, foreigners at times fear they will lose their reason, the heat being so unendurable.

An important condition in regulating the production of animal heat, and which may here be appropriately considered, is the influence of the size or bulk of the body of an animal as compared with its surface area; for the ratio of the bulk to the surface area being proportional to the size of the animal, and the heat produced being proportional about to the bulk, and the heat lost to the surface area, it follows that of two animals of similar shape but of different sizes, that, other things being equal, the larger animal of the two will lose relatively the least heat. Suppose, for example, of two animals of similar shape, that one be ten times as long as the other, then, while the loss of heat in the larger animal will be as its surface area 10^2, or 100 times as great as the small one, the heat produced by the larger animal will be as its bulk 10^3, or 1000 times as great. It follows, therefore, that if two such animals have the same temperature that the small animal either retains its heat much better than the large one or that it produces heat far more actively. That the latter is the case appears from the fact of a small animal taking more food relatively than a large one, and of its circulation and respiration being absolutely more frequent. Small animals are also more readily affected by changes in the external temperature than large ones, the temperature of a rabbit, for example, under such circumstances, varying more than that of a dog, that of a young animal more than that of an old one of the same kind, as that of

the young child, as compared with that of the adult. Large animals, like the whale or hippopotamus, live either habitually or temporarily in the water, the latter being a better conductor of heat than air. On the other hand, the smallest homoiothermal animals live in the tropics, while of animals of the same kind the largest ones live in temperate or cold regions. Of course, what has just been said with reference to the bulk and surface area in the production and loss of heat is not inconsistent with what daily observation teaches when man or animal changes the position of the body, for as the external temperature varies if the body, when cold, be contracted, less surface being then exposed less heat will be lost, whereas, if, when overheated, the body and limbs be stretched to the utmost, more surface being exposed, then more heat will be lost.

As a further illustration of the manner in which the production of heat is regulated in reference to climate, may be mentioned the well-known facts already alluded to, of the diet of the inhabitants of cold countries being so different from that of those of hot ones, the amount of food consumed by the former not only being greater, but the food consisting largely of fat and oil, substances eminently suitable for the production of heat. A corresponding difference in diet is also made use of by the inhabitants of temperate regions in winter, as compared with summer, and with the same effect of increasing the production of heat in cold and of diminishing it in hot weather. It might be supposed that a loss of heat, inducing an increased production, would be shown from the amount of oxygen absorbed and carbon exhaled, and notwithstanding the numerous difficulties incidental to such an experimental investigation, it may be said that the general result obtained by Lavoisier, Crawford, and De la Roche,[1] as well as by modern experimenters, as Rohring and Zuntz,[2] Colasanti,[3] Pflüger,[4] Prince Theodore,[5] Voit,[6] etc., was, as a rule, that the consumption of oxygen and exhalation of carbon dioxide increased with a fall in the external temperature and diminished with a rise in it, though, under certain circumstances, hot-blooded animals behaved as cold-blooded ones—that is, the absorption of oxygen and exhalation of carbon dioxide increase with a rise in the external temperature and diminish with a fall in it. Within certain limits at least, it may be said that, when a man or animal is exposed to cold, the production of heat is increased, as shown by the greater amount of oxygen absorbed and carbon dioxide exhaled, but when exposed to heat the reverse is the case and less heat is produced.

While we have seen that the heat produced by a man or animal is due to the oxidation of the food, there can be no doubt but that the regulation (thermotaxis), of heat production (thermogenesis), in relation to heat dissipation (thermolysis), is accomplished by the

[1] Op. cit.
[2] Pflüger's Archiv, 1871, iv., s. 57.
[3] Ebenda, xiv., s. 92.
[4] Ebenda, 1878, xviii., s. 247.
[5] Zeitschrift f. Biol., 1878, xiv., s. 51.
[6] Ebenda, s. 57.

nervous system. While the exact manner in which the production and dissipation of heat is influenced by the nervous system is as yet but imperfectly understood, recent researches render it highly probable that there exist what may be called thermogenic centers situated in the spinal cord and brain which receive impulses transmitted to them by afferent nerves from the periphery and emit reflexly impulses which are transmitted in a reverse direction to muscles, glands, blood vessels, etc. Indeed it is only by assuming the existence of some such nervous mechanism ; of thermo-inhibitory and thermo-accelerator centers, that we can explain many of the phenomena of animal heat just mentioned, such as for example, that a rise or fall in the external temperature causes a diminution or increase in heat production respectively.

CHAPTER XXV.

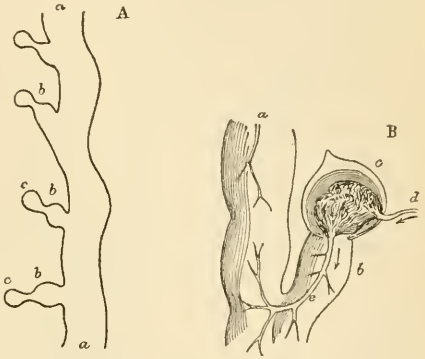
THE KIDNEYS AND URINE.

We have seen that during digestion the food is transformed into peptone, glucose, emulsified fats, etc., that through absorption and the circulation the latter are carried to the tissues, supplying the cells of the same with materials, which, either in being assimilated serve for repair, growth, or development, or in being destroyed are a source of energy; that the destructive metamorphosis going on in the body caused by fermentation, hydration, oxidation, etc., incidental to life, the final outcome of which, at least, is the production of carbon dioxide, water, and urea, is due, to a far greater extent, to the destruction of the food by the cells of the tissues than to the destruction of the tissues themselves; that, by means of the lungs, oxygen is introduced into the system, and carbon and water removed, the skin, as we shall see, in the latter respect, acting also, to a certain extent, in the same way. In concluding our account of nutrition, it remains for us still to consider the structure of the kidneys, and, so far as is known, the manner in which the urine is excreted by them from the system. It will be observed that we speak of the urine as being excreted by the kidneys, and it may be appropriately mentioned here that, while it would be equally correct to refer to the secreting as well as to the excreting of the urine, the word secretion, however, is usually made use of in referring to a glandular product of some use, such as the saliva, gastric juice, etc., the term excretion being confined to products of no use, to be gotten rid of, such as the urine. In this sense, the bile, as we have seen, is both an excretion and a secretion.

A kidney may be regarded, functionally, as consisting essentially of one or more tubes, opening externally at one end, but terminating internally at the other end in blind, sac-like capsules. The tubes and their capsules are lined with an epithelium, and covered more or less exteriorly with blood vessels, the latter supplying the tubes with blood, from which are excreted, by the cells of their lining epithelium, the urea, water, etc., constituting the urine; elaborated and transported by the cells into the interior, or lumen of the tubes, the urine passes finally thence out of the body. Such a disposition as that just described, obtains in the kidneys of the lower vertebrates. In bdellostoma, for example, one of the cyclostomous fishes, the kidney consists (Fig. 212, A) of a ureter (*a*), from which are given off, at right angles, short uriniferous tubules (*b*, *b*), terminating in capsular-like Malpighian bodies (*c*), lined

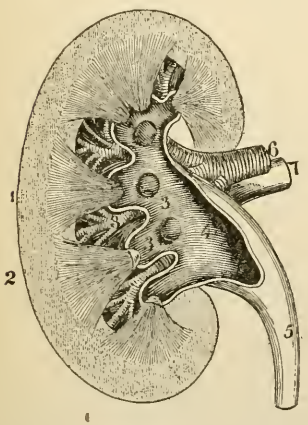
with an epithelium, and supplied externally with blood vessels (Fig. 212, B *d*, *e*). The kidneys in man, smooth, dark red, compressed, oval bodies, deeply set in the lumbar region, opposite the last dorsal and two or three upper lumbar vertebræ, present such a characteristic form through the presence of a deep notch on their inner side that the term reniform or kidney-form, derived from them, is often conveniently made use of in describing various other natural objects. If a kidney be divided longitudinally through its breadth (Fig. 213), it will be observed that the hilus or notch leads into a cavity, the sinus of the kidney, which is filled in the natural condition with the pelvis (4), or expanded upper portion of the ureter (5), and the renal vessels (6, 7) and nerves. Such a section further shows that the kidney consists apparently, at least, of two distinct substances, an internal striated portion, the medullary substance (2), and an external granular-looking portion, the cortical substance (1). This distinction is, however, a purely artificial one, being, in reality, due to the uriniferous tubule (Fig. 214), coursing, in its beginning (8). through the medullary or interior portion in a straight manner, but at its termination (5), in the cortical or external portion in a convoluted one. Theoretically, at least, if the uriniferous tubules, of which the kidney largely consists, could be unravelled and straightened out, the distinction of medullary and cortical substance would then cease to exist. It is, also, very apparent, as observable in a longitudinal section (Fig. 213), that the interior, or so-called medullary, portion of the kidney, is disposed in from ten to fifteen conical masses, the pyramids of Malpighi (2), so named after the celebrated anatomist of that name, the bases

Fig. 212.



Kidney of bdellostoma. The same magnified. (Muller.)

Fig. 213.



Longitudinal section of a kidney. 1. Cortical substance. 2. Renal pyramid. 3. Renal papillæ. 4. Pelvis. 5. Ureter. 6. Renal artery. 7. Renal vein. 8. Branches of the latter vessels in the sinus of the kidney. (Leidy.)

of which are imbedded in the cortical substance, while the free summits, or papillæ (3), of the same project into the sinus of the kidney. It may be mentioned in this connection that the Malpighian pyramids, together with the cortical substance enveloping each of their bases, the columnæ, or septa Bertini,[1] correspond to the dis-

FIG. 214.

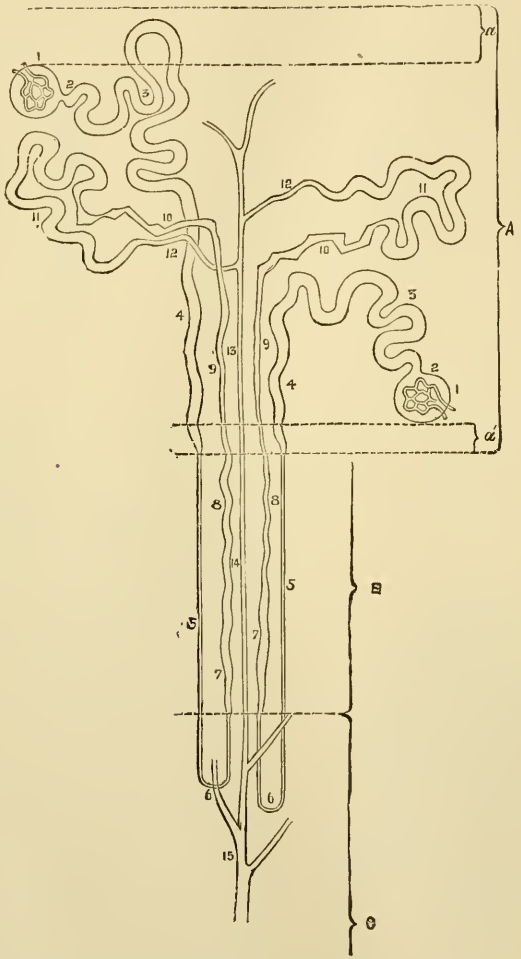


Diagram and course of two uriniferous tubules. A. Cortex. B. Boundary zone. C. Papillary zone of the medulla. *a*, *a'*. Superficial and deep layers of cortex, free from glomeruli.

tinct lobules of which the human kidney consists in the fœtal state, and while becoming indissolubly blended as development advances in man, remain quite distinct throughout life in many of the mammalia, as in the otter and bear among the carnivora, and in the

[1] Mem. de l'Acad. des Sciences, 1744, p. 77.

cetacea—whales, dolphins, for example. If now the apex or summit of one of the Malpighian pyramids, or papillæ, be examined microscopically, very minute orifices (between 200 and 500) will be observed, each of which is the beginning of a uriniferous tubule (Fig. 214), and which will be seen, if followed in longitudinal section, to pursue, as a tube of Bellini,[1] a nearly straight course through the medullary portion, as already mentioned, each Bellinian tubule, however, soon dividing and subdividing, the bundle formed by the division of the latter, at the beginning of the cortical substance, constituting the pyramids of Ferrein.[2] The uriniferous tubule followed thence outwardly toward the cortical substance, then turns back upon itself toward the medullary portion, and turning once more toward the cortical portion as the ascending and descending loops of Henle[3] becomes quite convoluted, constituting the cortical tubules of Ferrein,[4] terminating, finally, in a pouch-like dilatation, the capsule of Muller,[5] the latter, as we shall see, being inflected over the so-called Malpighian vascular glomerulus, the capsule and glomerulus together constituting a Malpighian corpuscle, as first described by Malpighi.[6]

The uriniferous tubules, held together by connective tissue, the stroma about 50 mm. (2 inches) in length, and with a diameter varying between the $\frac{1}{9}$ and $\frac{1}{24}$ of a millimeter ($\frac{1}{225}$ and $\frac{1}{600}$ of an inch), the Bellinian tubules being the largest, consist of basement membrane lined with epithelium; the latter, however, like the diameter of the tube, differing considerably according to the part examined, being, for example, distinct and columnar, with a wide lumen in the straight, or Bellinian tubules, but indistinct granular, with little or no lumen in the convoluted tubules, or tubules of Ferrein.

The kidneys are very vascular, the arteries being large vessels in proportion to the size of the organs which they supply. The renal artery (Fig. 213, 6), as it approaches the hilus of the kidney, subdivides into four or five branches, which, entering the sinus, pass thence between the pyramids into the substance of the kidney, dividing and subdividing as they ramify through the cortical substance, each branch finally terminating in an afferent vessel (Fig. 215, 1) leading to a Malpighian glomerulus, so called after their discoverer, Malpighi, around which, as already mentioned, as first shown by Bowman,[7] is inflected the capsule of Muller, or the end of the uriniferous tubule. Each Malpighian glomerulus (Fig. 215), about the $\frac{1}{4}$ of a mm. ($\frac{1}{100}$ of an inch) in diameter, including the investing capsule, consists of a close-set, spheroidal,

[1] Laurentii Bellini, Exercitatio anatomica de structura et usu renum, pp. 64–72, Fig. x. Amstelodami, 1665.

[2] Mém. de l'Acad. des Sciences, 1749, p. 284, pl. 14 and 15.

[3] Abhand. d. K. Ges. d. Wiss. zu Gottingen, 1862, x. [4] Op. cit.

[5] De glandularum secernentium structura penitiore, p. 101. Lipsiæ, 1830.

[6] Marcelli Malpighi, Philosophii et Med. Bon E. Soc. Reg. Operum, Tom. sec. Londini, 1686. De Renibus. [7] Phil. Trans., 1842, p. 57.

knot-like net of capillaries, from which emerge an efferent vessel 2, which, together with other efferent vessels, forms a capillary network (p) along and between the uriniferous tubules. From this network the renal veins (r) originate, which, converging, form the external surface of the kidney toward the bases of the pyramids, pass through the sinus, and, becoming confluent, emerge as one trunk (Fig. 213, 7) from the hilus. The water, urea, etc., having been excreted by the epithelial cells lining the uriniferous tubules from the blood brought to them by the renal artery, elaborated as the urine, passes down through the uriniferous tubules, finally dribbling out of their orifices situated, as already mentioned, at the apices or summits of the Malpighian pyramids (Fig. 213, 3), one or more of the latter projecting into one of the calices or infundibula, into which the pelvis or upper expanded portion of the ureter (4) (within the sinus) is subdivided, a further passage-way is provided by which the urine is conveyed to a temporary reservoir—the bladder—a musculo-membranous sac, from which it is finally eliminated during micturition from the body. The calices, pelvis of the ureter, and the ureter proper consist externally of a fibrous coat, of a middle unstriated muscular one, and internally of a lining mucous membrane. The fibrous layer of the calices at the base of the pyramid becomes continuous with that investing the sinus of the kidney, the latter, in turn, being a continuation of its external fibrous capsule; the middle muscular layer, thinning away at the pelvis, disappears altogether at the base of the pyramids, while the mucous membrane of the calyx is reflected upon the pyramids, becoming continuous at the orifice with that of the uriniferous tubule. It is evident, therefore, that leaving out of consideration the anatomical details just described, that a kidney, physiologically, may be regarded as consisting essentially of one or more uriniferous tubules, supplied with blood, a uriniferous tubule consisting of basement membrane separating blood on the one side from a secreting cell on the other. When reduced, therefore, to its simplest expression, the structure of the kidney does not differ in any way from that of glands in general.

FIG. 215.

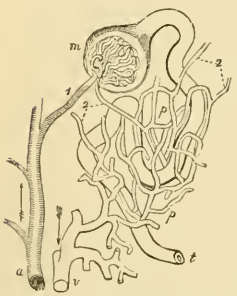


Diagram showing the relation of the Malpighian body to the uriniferous ducts and blood vessels. *a*. One of the interlobular arteries. 1. Efferent artery passing into the glomerulus. *m*. Capsule of the Malpighian body. *t*. Uriniferous tube. 2. Efferent vessels which subdivide in the plexus *p*, surrounding the tube, and finally terminate in the branch of the renal vein, *v*. (BOWMAN.)

Having studied the structure of the kidneys, let us consider now the manner in which the urine is secreted. That the latter is excreted but not elaborated by the kidneys to any extent appears not only from what has been learned of the origin of its constituents and of their accumulation after ligation of the renal arteries, extirpation of the kidneys, etc., but from the fact, also, that in certain

cases referred to by Haller,[1] Nysten,[2] Burdach,[3] and Laycock,[4] in which the kidneys were either congenitally absent or not acting, the urine, or fluid closely resembling it at least, was vicariously excreted by the skin, pleura, peritoneum, mucous membrane of the intestinal canal, salivary, lachrymal, and mammary glands, ears, nose, etc. Such being the case, the question for our consideration is the determination of the manner in which the different constituents of the urine are separated by the renal epithelium from the blood supplying the kidney.

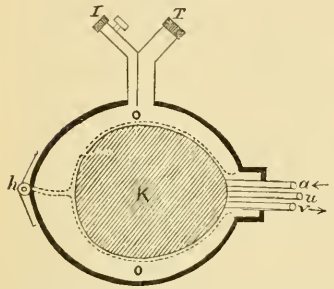
We have just seen that the kidney is made up of uriniferous tubules, each tubule consisting of two distinct portions, a tubular part and a capsular part, both lined with epithelium and supplied with blood vessels. The blood vessels invaginated by the capsular portion being, however, disposed in a capillary knot of far greater aggregate capacity than the branch of the renal artery from which it originates, and of the single exit vessel in which it terminates, the blood must be, therefore, retarded as it flows within the capsule, and the escape of its water much favored by such a disposition. That the function of the capsular part of the uriniferous tubule, as shown by Bowman, is to filter, drain off the water from the blood, the urea, etc., being excreted by the tubular part and then washed out, so to speak, by the water, is confirmed by what is seen in reptiles. Thus in the boa, uric acid, the equivalent of the urea of mammals, excreted in a solid state is only found in the tubular portion of the uriniferous tubule. The excretion of the urine will then depend essentially upon the relation of the pressure of the blood in the renal arteries, 120 to 140 mm. mercury, to that of the fluid within the tubules and ureter, 10 to 40 mm., the amount of urinary materials in the blood, and the activity of the renal epithelium. The influence of the blood pressure is shown from the fact that the excretion of urine is diminished with the lowering of the pressure of the blood whether brought about generally or locally, as, for example, by division of the spinal cord or stimulation of the splanchnic nerves; in fact, if the blood pressure falls as low as 40 mm. of mercury the excretion of the urine ceases. On the other hand, with the elevation of the blood pressure as induced by stimulation of the spinal cord or by division of the splanchnic nerves the excretion of the urine is increased.[5] Experimental investigation has shown, however, that the excretion of the urine varies not only with the pressure, but also with the quantity of blood flowing through the renal glomeruli. Thus, for example, in experiments made with excised kidneys, artificially supplied with

[1] Elementa Physiologiæ, Tomus ii., p. 370.
[2] Recherches de la Phys. et de Chimie, p. 265.
[3] Physiologie (Jourdain), Tomus viii., p. 248.
[4] Edin. Med. and Surg. Journal, 1838.
[5] The influence exerted by the spinal cord and splanchnic nerves upon the blood pressure in the kidneys will be better appreciated after the vasomotor nerves have been described.

blood, the amount of the secretion was found to depend more upon the rate of flow than upon the pressure.[1] It can be readily shown by means of the oncometer and oncograph that the secretion of the urine varies with the quantity of the blood flowing through the kidney.

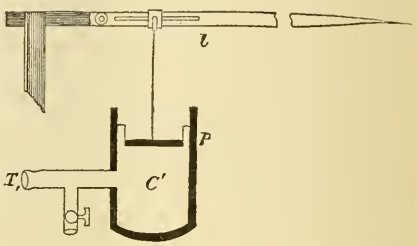
The oncometer (Fig. 216) is a metallic capsule, shaped like a kidney, composed of two halves moving on a hinge (*h*), by which the kidney is introduced, the renal vessels (*a*, *v*, *u*) passing out by

Fig. 216.



Oncometer. K. Kidney; the thick line is the metallic capsule. *h*. Hinge. *I*. Tube for filling apparatus. *T*. Tube to connect with T_1. *a*, *v*, *u*. Artery, vein, ureter. (Stirling, after Roy.)

Fig. 217.



Oncograph. *C'*. Chamber filled with oil, communicating by T_1 with *T*. *p*. Piston. *l*. Writing lever. (Stirling, after Roy.)

the opposite opening. The kidney (K) is surrounded with a thin membrane, and the space (o) between the latter and the inner surface of the capsule filled with warm oil introduced through the tube *I*, which can be closed with a stopcock. The tube *T* being adapted to the tube T_1 leading into the metallic chamber *C'* of the oncograph (Fig. 217), also filled with oil, any increase in the volume of the kidney will force the oil from the space o into the chamber *C'*, and the piston *p* will be elevated, and with it the recording pen. On the other hand, any diminution in the volume of the kidney through stimulation of the vaso-constrictor nerves will cause the oil to flow from *C'* into o, and the piston and with it the recording pen will fall. By adapting the pen to the cylinder we can get a trace of the so-called kidney curve (Fig. 218).

Fig. 218.

Trace obtained by oncograph.

The kidney having been placed within the oncometer and a canula placed into the ureter so as to measure the outflow of the urine, it will be observed that as the volume of the kidney contracts through stimulation of the vaso-constrictor nerves, the excretion of the urine di-

[1] I. Munk, Virchow's Archiv, Band iii., 1888, s. 434.

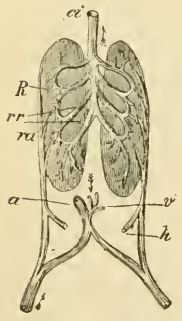
minishes, whereas when the volume of the kidney expands through division of the vaso-constrictor nerves the excretion of the urine increases. That the renal epithelium exerts, however, an excretory activity independent of the pressure and quantity of the blood, is shown by the experiments of Heidenhain[1] upon animals in which, after the flow of urine had ceased through section of the spinal cord below the medulla, sodium sulphoindigotate being injected into the veins was found, after death, in the renal epithelium or the interior of uriniferous tubules according to the length of time elapsing between the injection and killing of the animals, proving that the renal epithelium had excreted the sulphoindigotate from the blood. By varying the quantity of the salt injected and the time elapsing between the experiment and the subsequent examination, Heidenhain was able to follow step by step the salt as it passed from the blood into the cells, thence through the latter into the tubules for some little distance. There being no fluid passing along the uriniferous tubules to wash away the sulphoindigotate, the latter remained about where it had been excreted. Not a trace of the salt injected could be found in the epithelium or within the capsular portion of the tubule, the cells excreting the sodium sulphoindigotate being of the kind described by Heidenhain as rod-shaped, more especially found in the intercalary portion of the uriniferous tubule. It was also shown by these experiments, as might have been expected, that there was a limit to the excreting capacity of the renal epithelium, the excretion of a second quantity of sulphoindigotate injected soon after the first being very imperfect. It might be supposed that the experiments of Heidenhain with sulphoindigotate could be repeated with urea, uric acid, etc., with the view of showing that these substances are excreted by the cells lining the tubular and not by those lining the capsular portion of the tubule. Inasmuch, however, as the injection of urea, etc., gives rise to a copious flow of urine, even after section of the spinal cord below the medulla, which is not the case with the sulphoindigotate, the urea will be washed along the tubules as fast as it is excreted, which makes it impossible, therefore, to say by what part of the renal epithelium it has been excreted. It is well known, however, that in birds, reptiles, and fishes, branches from the mesenteric, femoral veins, etc., pass to the kidneys (Fig. 219), and after ramifying through the latter converge and finally terminate in the vena cava, the veins being known collectively as the renal portal system, or the system of Jacobson,[2] after their discoverer. The blood flows through the kidneys in these animals, therefore, very much as it does through the liver in man. Now the branches of this renal portal system, together with the efferent vessels from the glomeruli, constitute the capillary plexus surrounding the tubular portion of

[1] Hermann, Physiologie, Funfter Band, Erster Theil, s. 345.

[2] De systemate venoso peculiari in penultis animalibus observatio. Copenhagen, 1821.

the uriniferous tubules, the glomeruli themselves, however, being supplied exclusively by branches of the renal artery. It is obvious, therefore, that if the renal artery be ligated the blood will be entirely cut off from the glomerulus, while that supplying the remaining portion of the uriniferous tubule will be unaffected. Such being the case, it follows that if urea still appears in the urine after ligation of the renal arteries, it must be excreted by the epithelium of the tubular and not by that of the capsular portion of the uriniferous tubule. These theoretical considerations are fully borne out by the experiments of Nussbaum,[1] who has shown that while sugar, peptones, and albumin are excreted by the glomeruli, these substances not appearing in the urine after ligation of the renal arteries, urea is excreted by some part of the remaining portion of the tubule, urea, when injected into the blood, giving rise to a flow of urine even after ligation of the arteries.

Fig. 219.



c i. Vena cava. *R*. Kidneys. *r r*. Vena revehens. *r a*. Vena advehens. *a*. Vena epigastrica. *h*. Vena hypogastrica. *i*. Vena ischiada. *v*. Vesical veins. (Gegenbaur.)

The recent experiments of Schroeder[2] and of Dreser[3] made with sodium chloride, potassium nitrate, caffein, etc., prove also that the increased flow of blood through the kidney after the taking of these substances is due largely to some specific action of the renal epithelium and more especially to that covering the glomeruli.

The urine, like the bile, is excreted continuously, and while the flow may be increased or diminished, it never absolutely ceases in health for any length of time. The urine trickling through the mouth of the uriniferous tubules into the calices, passes thence by the ureters into the bladder, its return from the latter during micturition being prevented by the obliquely disposed valvular-like orifices of the ureters.

The bladder is a musculo-membranous sac, the muscular fibers, chiefly of the involuntary character, being disposed in a longitudinal and circular manner, the former constituting the detrusor, the latter the sphincter vesicæ, by the contraction of which the urine is either expelled or retained within the bladder. Micturition appears to be brought about essentially as follows:

During the intervals in which the urine is not voided the sphincter vesicæ is in a state of tonic contraction; if, however, the urine be retained for some time the contraction of the sphincter alone is insufficient to resist the outflow, and the action of the adjacent muscles is called upon to assist it. The disposition to urinate after a time becoming very great a few drops of urine pass into the

[1] Pflüger's Archiv, 1877, xvi., s. 139; 1878, xvii., s. 580.
[2] Archiv für exp. Path. u. Pharm., Band xxiv., 1888, s. 85.
[3] Ebenda, Band xxix., 1892, s. 303.

urethra, the impression so produced then calls into play the action of the detrusor and ejaculator urinæ, the sphincter being simultaneously relaxed, and the bladder is emptied. Ordinarily the voiding or the retaining of the urine is a voluntary act, but that the urine can be voided at regular intervals independent of the will is shown by the regularity with which the action is performed in animals in which the spinal cord has been divided, and in human beings in which it has been injured. The mechanism by means of which the muscular contractions are brought about in response to stimuli, the result of which is the voiding of the urine, will be better appreciated after the subject of reflex action has been considered.

The Urine.

The urine is a clear, amber-colored fluid, of a watery consistence, containing a little mucus, saltish in taste, with a characteristic though not disagreeable odor, acid in reaction, and with a specific gravity varying between 1.020 and 1.025. The color of the urine appears to be due to a mixture of urobilin or its mother substance, urobilinogen, and of several other pigments whose nature is as yet but imperfectly understood. The coloring matter of the urine appears to be identical with hydrobilirubin ($C_{32}H_{44}N_4O_7$), the so-called urobilin being that part of the hydrobilirubin derived from the bilirubin of the bile which being absorbed passes out of the body in the urine rather than in the feces. The varying tints often observed in the urine from an amber color to red are probably due to the oxidation of this substance.

Acidity of Urine.

The acidity of the urine is not due to free acid, as can be shown by there being no precipitate formed on the addition of sodium hypophosphite, but to the presence of the acid sodium phosphate (NaH_2PO_4), the latter salt being probably formed by the reduction of the basic sodium phosphate (Na_2HPO_4) of the blood, by abstraction of one equivalent of its sodium, by uric, or hippuric acids, sodium urate, or hippurate, being formed, as may be seen from the following formula, for example :

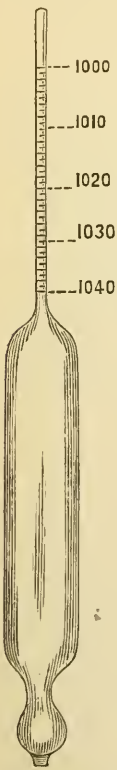
Sodium phosphate.		Uric acid.		Acid sodium phosp.		Sodium urate.
$2Na_2HPO_4$	+	$C_5H_4N_4O_3$	=	$2NaH_2PO_4$	+	$Na_2C_5H_2N_4O_3$.

The acidity of the urine, due to acid sodium phosphate, as measured by the amount of a standard solution of caustic soda necessary to neutralize it, is equivalent to about two grammes of oxalic acid in twenty-four hours, supposing the urine voided in that time to amount to 1200 c. cm. The solution of soda, of such a strength that each cubic centimeter, containing 0.0031 gramme of soda, exactly neutralizes 0.0063 gramme of oxalic acid, is added, drop by drop, to a given quantity of urine—say 100 c. cm., until

litmus paper changes violet in color, *i. e.*, neither to red nor blue. The number of cubic centimeters of the soda solution, as read off on the burette, say 30, when multiplied by 0.0063 gramme, will give then the amount of acidity, or 0.1890, in 100 c. cm. of urine, as measured in grammes of oxalic acid, and, consequently, of 2.2 grammes in 1200 c. cm.

Specific Gravity of the Urine.—The specific gravity of the urine, a matter of great importance practically, is readily determined by the urinometer (Fig. 220), the stem of which is so graduated that when immersed in water the level of the latter stands at that portion of the stem marked 1000, the level at which the urine stands, as read off on the urinometer when the latter is immersed in the urine giving the specific gravity sought. A convenient method of determining the solids of the urine, approximately, at least, is by means of what is generally known as Trapp's, or Christison's, formula, based upon the fact, as empirically shown by that chemist, of the specific gravity of the urine bearing generally a close relation to the solid matters which it contains in solution. The rule is as follows: Multiply the last two figures of a given specific gravity expressed in four figures—say 1.022, by 2.33; the result, $22 \times 2.33 = 51.26$ grammes, will be the amount of solids contained in 1000 parts of urine having a specific gravity of 1.022, and if the urine passed in twenty-four hours amounts to 1200 c. cm., then the solids will be increased proportionally, $1000 : 1200 :: 51.26 : x = 61.51$ grammes. If the specific gravity of the urine be below 1.018, greater accuracy will be obtained by multiplying by 2 instead of 2.33. On the supposition that 1500 c. c. of urine are voided in the twenty-four hours, the solids are usually found to amount to 60 grammes (926 grains) or 40 grammes of solids per 1000 c. c. of urine.

FIG. 220.



Urinometer. (LANDOIS.)

The daily quantity of urine excreted amounts in the adult man, on the average, according to Parkes,[1] who has compared the observations of many observers, to about 1575 c. c. (fifty-two and a-half fluid ounces). As little as 1050 c. c. (thirty-five ounces), and as much as 2430 c. c. (eighty-one ounces) may, however, be voided within the limits of health, and it may be added that almost every intervening number between these limits has been given as the usual average, the very greatest difference prevailing in this respect. Apart, however, from personal peculiarities, the amount of urine excreted is also influenced by sex, age, and season of the year.

[1] The Composition of the Urine, p. 5. London, 1860.

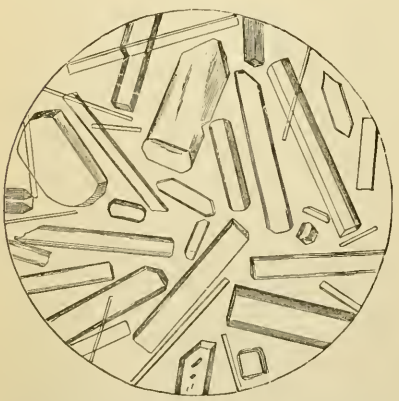
Thus, less (1200 c. c.) urine is excreted by women than men, more by children, relatively to their weight, than by adults; more in winter, the skin being then less active, than in summer. When it is considered that the quantity and quality of the urine, as we shall see, are influenced by such conditions as wakefulness, sleep, rest, exercise, solid and liquid food, it might be naturally supposed that considerable differences would present themselves in the urine passed at different times during the day, usually five or six times within the twenty-four hours. As a matter of fact, diurnal variations do succeed each other quite regularly. Thus, the urine collected during the night and voided early in the morning is strongly colored, distinctly acid, and of a high specific gravity; toward noon it becomes paler, less dense (1.003 to 1.008), and less acid, the acidity even disappearing altogether; during the afternoon and evening the color, density, and acidity increase, while by night it has become again highly colored, markedly acid, and with a specific gravity of 1.028 or even 1.030. As these diurnal variations are, however, increased or diminished by the amounts of liquids taken, and as the acidity of the urine is inversely as that of the stomach, and may be more or less neutralized by fruits, vegetables, etc., the lactates, malates, and tartrates of the same being replaced within the system by carbonates, and reappearing in that form in the urine, it is evident that if the acidity and specific gravity are to be determined, one sample voided will not suffice, but that the entire quantity passed in twenty-four hours should be examined, and the mean result taken. It is worth while mentioning that with reference to the liquids absorbed by the system or lost, that under normal conditions the relation of the specific gravity of the urine to that of the liquids is an inverse one. Thus, if a great quantity of liquid be taken, or the perspiration be diminished, the amounts of solids remaining the same, the specific gravity of the urine will be diminished, whereas, if drinks be abstained from, or the perspiration be increased, the specific gravity will be increased. If, however, notwithstanding that a great quantity of liquid be absorbed, the specific gravity still remains high, or with a diminution in the liquid the specific gravity remains low, there would be reason to suspect disease through the increase or diminution respectively in the solid constituents of the urine, and such would also be the case if, the specific gravity remaining constant, the quantity of urine increased or diminished, and *vice versâ*. The urine, conveying out of the economy many inorganic and organic constituents, is a highly complex fluid, and, varying much as regards its constituents, it is difficult, if not impossible to give its composition.

COMPOSITION OF THE URINE ACCORDING TO PARKES.[1]

Constituents.	By an average man of 66 kilo.	Per 1 kilo of body weight.
Water	1500.000 grammes	23.000 grammes
Total solids	72.000 "	1.100 "
Urea	33.180 "	0.500 "
Uric acid	0.555 "	0.0084 "
Hippuric acid	0.400 "	0.0060 "
Creatinin	0.910 "	0.0140 "
Pigment and other substances	10.300 "	0.1510 "
Sulphuric acid	2.012 "	0.0305 "
Phosphoric acid	3.164 "	0.0486 "
Chlorine	7.000 (8.12) grammes	0.1260 "
Ammonia	0.770 grammes	. . . "
Potassium	2.500 "	. . . "
Sodium	11.090 "	. . . "
Calcium	0.260 "	. . . "
Magnesium	0.207 "	. . . "

Urea.—Urea (CON_2H_4), the most important constituent of the urine, is regarded by chemists, as already mentioned, as being carbamide or the diamide of carbon dioxide, its chemical composition being expressed by the formula $CO\begin{cases} NH_2 \\ NH_2 \end{cases}$. Urea is a colorless neutral substance very soluble in water and boiling alcohol but insoluble in ether, and crystallizing in four-sided prisms (Fig. 221).

FIG. 221.



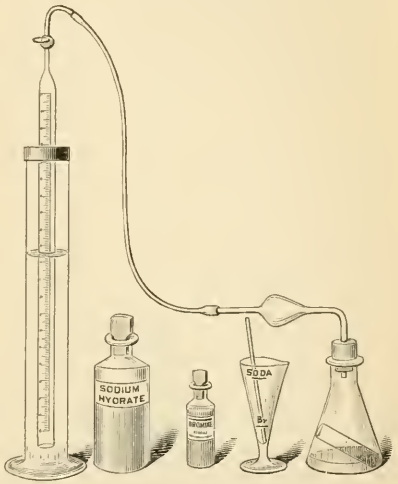
Urea, prepared from urine, and crystallized by slow evaporation. (LEHMANN.)

Urea can be readily obtained from the urine in the following manner: Add, say, 1.5 c. c. of pure nitric acid to 3.5 c. c. of concentrated urine in a watch glass and set aside to cool. The nitrate of urea then formed will be precipitated as a yellow crystalline mass. The insoluble nitrate caught on a filter, dried, and dissolved in boiling water, is mixed with animal charcoal to remove coloring matters and filtered while hot. The filtrate being then allowed to cool, colorless crystals of nitrate of urea will be deposited. The latter being dissolved in boiling water and barium carbonate added as long as effervescence takes place, barium nitrate and urea will be produced, from which after evaporating to dryness the urea can be extracted with absolute alcohol. On evaporating the alcoholic solution of urea crystals of pure urea are obtained. The amount of urea is usually determined by Davy's method which is based upon the decomposition of urea into water, carbon dioxide, and nitrogen by an alkaline

[1] Op. cit.

solution of sodium hypobromite, the amount of urea being determined from the nitrogen set free. As the urine contains, however, other nitrogenous constituents than urea, such as urates and creatinin, which will also be decomposed with the liberation of nitrogen, the urates must be removed by acetate of lead followed by sodic phosphate and the creatinin by an alcoholic solution of zinc chloride, otherwise the nitrogen produced would represent not only that derived from the urea (90 per cent.), but that from the remaining nitrogenous constituents (10 per cent. or more). The experimental procedure in making use of Davy's method for the determination of the urea in the urine is as follows: A given quantity of a solution of sodium hypobromite freshly made (100 gr. of caustic soda in 250 c. c. of water to which are added 25 c. c. of bromine) is introduced into the pyramidal-shaped vessel (Fig. 222), into which is placed a test-tube containing, say, 5 c. c. of urine. The pyramidal-shaped vessel being then inclined, the urine will mix with the solution of sodium hypobromite, and the urea will decompose, with the production of carbon dioxide. The latter will combine with the soda which is in excess, and will be retained in the mixture, while the nitrogen set free will pass over into the graduated burette standing in mercury where it can be collected and measured. The reaction is as follows:

Fig. 222.



Ureameter. (Landois.)

$$CON_2H_4 + 3(NaBrO) + 2(NaOH) = 3NaBr + Na_2CO_3 + 3H_2O + 2N$$

Let us suppose that the nitrogen obtained from the decomposition of the urea amounted, when corrected for temperature and pressure, to 40 c. c., the urea in 5 c. c. of urine would amount to 0.108 of a gramme,[1] and in 1500 c. c. of urine, to 32.4 grammes. It may be mentioned in this connection that the total amount of nitrogen in the urine is estimated by the Kjeldahl method.[2] This consists in heating the urine (5 c. c.) with an excess of concentrated or fuming sulphuric acid (40 c. c.) until all the nitrogen has been converted into ammonia and after caustic soda has been added in excess distill-

[1] 1 gramme of urea contains 0.46 of a gramme = 372.5 c. c. of nitrogen or 0.0027 of a gramme of urea = 1 c. c. of nitrogen and $0.0027 \times 40 = 0.108$ gramme.

[2] Zeits. für Analyt. Chemie, Band 22, 1883, s. 366.

ing the ammonia into sulphuric acid $\left(\frac{n}{10}\right)$ which has been previously titrated with soda $\left(\frac{n}{5}\right)$, the nitrogen being estimated from the amount of sulphuric acid that combines with the ammonia. Suppose, for example, that 18.6 c. c. of sulphuric acid have combined with ammonia as determined by titration, then as 1 c. c. of sulphuric acid corresponds to 0.0028 of a gramme of nitrogen,[1] the latter would amount in 5 c. c. of urine to 0.052 of a gramme ($18.6 \times 0.0028 = 0.052$) and in 1500 c. c. of urine to 15.6 grammes. If to this amount of nitrogen there be added the 0.94 of a gramme contained in the feces we obtain 16.5 grammes as the total nitrogen eliminated by the body in twenty-four hours, and which, when multiplied by 6.25[2] gives 103.2 grammes as the amount of proteid destroyed in the same period of time. While the urea excreted by an adult amounts upon an average in 24 hours to about 33 grammes (509 grains) it should be mentioned that the quantity excreted varies very considerably according to the age, weight of the body, sex, period of the day, season, and kind of food. Thus, children of from three to seven years of age with a weight of only one-fifth that of an adult may excrete in 24 hours as much as 15.5 grammes (240 grains). As might be expected, therefore, the amount of urea excreted continues to diminish as age advances. It would appear that less urea is excreted by the female than the male in the proportion, perhaps, of about half a grain less in the female for each pound of body weight, and that the amount is diminished during menstruation. The hour of the day apparently also exerts an influence upon the excretion of urea, the greatest amount being eliminated after breakfast and tea, the least during the night. The increase or decrease observed may be, however, due, to a certain extent, as we shall see, to the taking of or the abstaining from food. Like the urine, more urea is probably eliminated in cold than in warm weather.

It is difficult, if not impossible, however, to give exact numerical estimates. According to Dr. E. Smith,[3] the daily variations amounted in himself in a year to from 14 to 45 grammes (219 to 700 grains).

Of the conditions influencing the production of urea, none is so important as that of the taking of food. This becomes at once evident when the amount of urea excreted upon a vegetable or mixed diet is compared with that of a highly animal one. Thus while the urea excreted by Ranke,[4] during 24 hours on a vegetable diet amounted to 17 grammes (264 grains) and on a mixed one to between 30 and 33 grammes (463 to 617 grains) on a highly animal diet it was increased to as much as 86 grammes (1332 grains), or nearly

[1] Neumeister, op. cit., s. 670.
[2] Proteid : Nitrogen :: 100 : 16.
$$\text{Proteid} = \text{N} \times \frac{100}{16} = 6.25.$$
[3] Proc. of Royal Soc., May 30, 1861.
[4] Physiologie, 1872, s. 196, 504.

three times as much as normal. From such facts as that nearly all of the nitrogen of the food consumed passes out of the body in the form of urea in the urine, each gramme of urea implying the disintegration of 3 grammes of nitrogenous matter, or about 15 grammes of meat, and that the amount of urea excreted attains its maximum within five to seven hours after the taking of food, it would appear that by far the greatest amount of the urea produced must be derived directly from the disintegration of the nitrogenous food rather than of the tissues. It would be absurd to suppose that of the five pounds of meat eaten by a large dog, to take an extreme instance, the nitrogenous matter of the same should be first transformed into tissue, then decomposed into urea, and eliminated by the kidneys within the short space of 24 hours.

If the above view of urea being derived from nitrogenous food rather than nitrogenous tissue be accepted, it is readily understood why muscular exertion does not increase, as was once supposed, the production of urea, for muscular energy, being like all other kinds of so-called vital energy, transformed heat, and the latter being developed, if not exclusively, at least to a greater extent out of fats and carbohydrate than albuminous food, it follows that muscular activity will be measured not by the amount of urea but by that of the carbon dioxide produced. Such theoretical considerations are fully borne out by experiments.

Thus, for example, in the ascent of the Faulhorn by Wick and Wislicenus[1] involving considerable muscular exertion so far from the urea being increased by the exercise, it was actually diminished, which is in accordance with the fact, however, that no albuminous food had been taken for seventeen hours previous to the ascent, the diet of Fick and Wislicenus consisting of cakes made out of fat, starch, and sugar. Such being the case it is not strange that the amount of urea excreted should have been small, it being derived from the nitrogenous tissues of the body, the latter supplying the nitrogenous food that would have been otherwise present had the diet been a mixed one. It is well known that, even in starvation, more urea is excreted than on a diet consisting of sugar, fat, etc., since the latter substances, in supplying ready materials for combustion, spare the tissues of the body.

That there is an enormous amount of potiential energy locked up latent, so to speak, in sugars, etc., is made evident in the extreme weakness and emaciation so noticeable in diabetes, since the sugar in that disease, instead of being burned, and constituting as normally a source of heat and energy, passes unoxidized out of the body. The amount of energy lost to the system under such circumstances may be judged of when it is remembered that in extreme cases of diabetes as much as 40 ounces of sugar are passed in the urine in twenty-four hours, and that if the 16 ounces of carbon contained in such an amount of sugar were oxidized, heat enough

[1] London Phil. Magazine, 1866, p. 485.

would be produced, if applied mechanically, to raise 20 millions of pounds 1 foot high, or carry a man weighing 130 pounds on a level 66 miles. The system being deprived, therefore, in this disease of such a source of force, draws upon the albuminous tissues, hence the characteristic emaciation and weakness.

Essentially the same result was obtained by Haughton,[1] who found, while walking five miles a day, that the urea eliminated amounted to 501.28 grains; that when the walk was increased to 20.74 miles a day, and kept up for five consecutive days, the urea eliminated amounted to only 501.16 grains, or actually less. Parkes[2] found, also, that in the case of two soldiers, who walked in two days 56 miles on a non-nitrogenous diet, that the total increase of nitrogen eliminated amounted, in the one case, to only about 3 grains; and, in the other, 15 grains; corresponding to an increase of 6.4 grains, and 32.1 grains of urea, respectively, in forty-eight hours. The case of Weston, who walked over 300 miles in five consecutive days, cited by Flint[3] as an illustration of urea being increased by muscular exercise, illustrates really only what we have already seen to be the case, that the amount of urea excreted is greatly increased upon a highly nitrogenous diet, and that heat, the ultimate source of muscular force, can be developed through the combustion of nitrogenous, as well as of fatty or carbohydrate foods, the former means of obtaining the necessary heat being, however, a far more expensive way than the latter, and entailing greater work upon the system. It is true that, if the coal gives out, the steamer can be supplied with fuel from its masts, shrouds, etc., and other integral parts of its structure; one does not resort, however, save in dire necessity, to such a source of fuel. The facts of the case of Weston, just referred to, are essentially as follows: Weston walked in five consecutive days 310 miles, losing in weight 3¼ pounds. 1173.80 grains of nitrogen were taken into the system in the food, and 1807.60 grains were eliminated from it in the excreta, leaving 633.80 grains of nitrogen to be accounted for, which were evidently derived from the 3 pounds of tissue lost, the latter containing 633.80 grains of nitrogen; the remaining quarter of a pound, lost in weight, probably being due to the combustion of fat and elimination of water. Such being the case, and Weston having, therefore, little, if any, superfluous fat or carbohydrate matter at disposal for the production of heat or force, it would appear, from the large quantity of nitrogen eliminated, that his nitrogenous tissues were largely drawn upon to supply, through combustion, the heat incidental to the production of such a muscular effort. The 3 pounds of muscular tissue lost by Weston during the walk, supplied, therefore, the body with 3 pounds of nitrogenous food, which, in being consumed, accounted for the elimination of 633.80 grains of nitrogen, corresponding to 1124 grains of urea, just as if he had eaten 3 pounds

[1] British Med. Assoc., 1868. [2] Proc. Royal Soc., 1867, No. 89, 94.
[3] New York Medical Journal, 1871, p. 687.

of butcher's meat, instead of the same amount of his own body. That this conclusion is not merely a theoretical one is shown by the fact of Rubner,[1] weighing 72 kilo., being able to consume 1.30 kilo. (2.8 pounds) of meat, of which more than 98 per cent. were perfectly destroyed in the system with the production of the corresponding amount of nitrogen. It has also been shown by Voit[2] that in the case of a dog working on a tread-wheel and in that of man doing work in the respiration apparatus, that the energy expended was greater than that derived from the disintegration of nitrogenous substances, and that the urea excreted was within certain limits, at least, the same during rest and the performance of work. It should be mentioned, however, that some difference of opinion still prevails among physiologists as to the influence exerted by muscular work upon the excretion of nitrogen, the latter, according to Argutinsky[3] for example, being increased by muscular work. It appears, however, that in the experiments performed by this observer, which consisted in taking long walks, climbing mountains, the diet was deficient in carbohydrates, fats, which, necessitating the disintegation of nitrogenous material that would not have been drawn upon had the diet been a normal one, accounts for the increase of nitrogen very much, as in the case of Weston just referred to.

Not only has it been held that muscular activity increases the amount of urea, but mental and sexual activity as well. Even if such is shown, hereafter, to be the case, apart from the influence exerted by nitrogenous food, the facts are, at present, too few to justify giving any exact numerical estimate. It would appear, from what has just been said with reference to the production of urea, that, to a large extent at least, it is derived directly from the nitrogenous principles of the food without the latter becoming first tissue.

It will be remembered that, in considering the functions of the liver,[4] many facts were mentioned in favor of the view that leucin, tyrosin, etc., amide products of pancreatic digestion, were converted into ammonium carbonate or carbamate, and, being carried to the liver, were there transformed by a process of dehydration into urea.

Ammonium carbonate. Water. Urea.

$$(NH_4)_2CO_3 - 2H_2O = CON_2H_4$$

Ammonium carbamate. Water. Urea.

$$CO_2N_2H_6 - H_2O = CON_2H_4$$

In addition to the facts already offered in favor of the view that urea is produced in the liver, and somewhat in the manner just described, it may be also mentioned that more urea is found in the liver than in any gland in the body,[5] that in acute yellow atrophy

[1] Zeits. für Biologie, Band xv., 1879, s. 122.
[2] Hermann, Handbuch, Band vi., 1 Theil, 1881, ss. 189, 192.
[3] Pflüger's Archiv, Band 46, 1890, s. 552.
[4] See p. 150.
[5] Centralblatt med. Wiss., 1870, s. 249.

of the liver the urea of the urine is replaced by leucin and tyrosin, and that feeding animals with leucin increases the excretion of urea.[1] Admitting that by far the greatest quantity of urea is produced in the liver, it must be remembered that urea is not only found in the liver, but in many other parts of the system—in the chyle, saliva, blood, serous fluids, etc., and that in starvation in the absence of all food, though the amount of urea is gradually diminished, it is nevertheless present, even to the last. Of course, in such cases, one part of the body being nourished at the expense of another, the nitrogenous tissues, instead of food, supply the materials for the development of urea. That such is the case is shown by an experiment of Schöndorff,[2] who observed that while there is no increase of urea in the blood of a fasting dog irrigated through the limbs of a well-fed one, there is a very decided increase of urea in the blood that has passed through the limbs, if the latter be irrigated through the liver, the blood taking up some substance from the tissues which requires the action of the liver cells to be converted into urea.

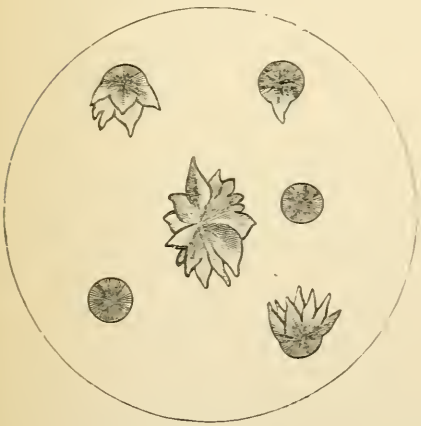
Urea being found under normal circumstances in many parts of the system, and being derived in starvation from the tissues, it is reasonable to suppose that part of the urea is also derived from the latter, even when nitrogenous food is taken, and since leucin and tyrosin are found in the thyroid, thymus, parotid, and submaxillary glands, kidney, liver, and suprarenal capsules, as well as in the pancreas and spleen, analogy would lead us to suppose that they may be antecedents of the urea derived from tissue, as we have supposed them to be of the urea derived from food. In this connection it is an interesting fact that while urea is not found in the muscles, spleen, or nervous tissue, creatin ($C_4H_9N_3O_2$) enters into the composition of muscles to the extent of two per cent., and into that of the spleen and probably of nervous tissue also. Now, since creatin, through dehydration, readily becomes creatinin ($C_4H_7N_3O$), and the latter through oxidation, urea (CON_2H_4), it is quite probable that creatin may be an antecedent of urea arising out of the disintegration of the muscular tissues, etc., but converted into urea elsewhere. It should be mentioned, however, that the creatin, or rather creatinin, normally found in the urine is not derived from the muscular tissue of the body, but from the food, since it varies in quantity, increasing with a meat diet, but not with exercise, and is absent in starvation. On the supposition that urea, whether derived from food or tissue, is not elaborated by the kidneys, but simply excreted out of the blood brought to them, we might expect to find that the blood of the renal artery contained more urea (0.03 per cent.) than that of the renal vein (0.01 per cent.), but also with the extirpation of the kidneys, or the ligation of the ureters, which has practically the same effect, that the urea would accumulate in

[1] Schultzen and Nencki, Zeit. für Biologie, 1872.
[2] Pflüger's Archiv, Band 54, 1893, s. 420.

the blood. Such indeed has been found experimentally to be the case, Voit[1] obtaining after extirpation of the kidneys in an animal 5.3 grammes of urea, or almost the same amount as would have been normally excreted (5.8 grammes) in the same time. It may be mentioned that the toxic effects appearing under such circumstances appear to be due not so much to the accumulation of a great quantity of urea as to the retention within the system of other undefined proteid substances.

Uric Acid.—Of the remaining constituents of the urine, uric acid ($C_5H_4N_4O_3$) is the most important, it being like urea, one of the forms in which nitrogen leaves the economy. Indeed, in reptiles and birds, uric acid is the principal form in which nitrogen is eliminated. Uric acid existing in the urine in the form of urates, usually as a brownish-yellowish, powdery substance; ammonium or sodium urate (Fig. 223) may be readily obtained by the decomposition of the same. Thus, if nitric or hydrochloric acid be added to freshly filtered urine in the proportion of about two per cent. by volume,

Fig. 223.



Sodium urate from urinary deposit.

Fig. 224.

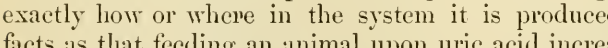
Uric acid, deposited slowly from urine.

and the mixture be allowed to remain at rest, within twenty-four hours uric acid will be deposited as thin crystals on the sides of the vessel. These crystals (Fig. 224) are usually transparent, yellowish, rhombic plates, with the angles rounded off, and are frequently collected together in rosette, star-like clusters and spheroidal masses.

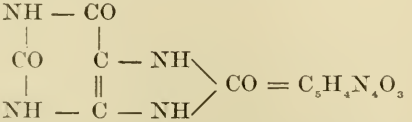
The crystalline forms of uric acid are, however, very variable, depending upon the concentration of the solution from which they are obtained, the rapidity with which they are formed, and whether they are separated out spontaneously or by the addition of acids to the urine. Uric acid when freed from impurities is a colorless, crystalline powder, tasteless and without odor. If uric acid be

[1] Centralblatt med. Wiss., 1868, p. 468.

boiled with nitric acid it dissolves with a yellow color, and with an abundant liberation of gas. If the solution be now evaporated a brilliant red stain is left, which by the addition of aqua ammonia, becomes purple. The presence of uric acid and urates can be readily determined by this procedure, which is usually known as the murexide test. The amount of uric acid in the urine can be determined approximately, at least, by Haycraft's method.[1] This consists in making the urine first alkaline; precipitating with an ammoniacal silver solution, dissolving the precipitate on nitric acid (30 p. c.) and then titrating the solution with a $\frac{n}{100}$ sulpho-cyanide solution, 1 c. c. of the solution corresponding to 0.00168 grammes uric acid. The uric acid excreted in human urine amounts on the average during twenty-four hours upon a mixed diet to about 0.7 grammes (11 grains). The amount eliminated varies considerably, however, with the kind of food taken, 0.5 grammes (8 grains) upon a non-nitrogenous diet, 2 grammes (31 grains) upon a nitrogenous one, and 0.2 grammes (0.3 grains) during starvation, the body supplying in the latter case the nitrogenous material. It would appear, therefore, that uric acid like urea is derived from the disintegration of nitrogenous food rather than of tissue. Uric acid is not only found in the urine but also in small amounts in the spleen, lungs, heart, pancreas, liver, blood (especially in gout). While uric acid like urea is derived from nitrogenous tissue or food, considerable difference of opinion still prevails among chemists as to exactly how or where in the system it is produced. From such facts as that feeding an animal upon uric acid increases the amount of urea excreted, the uric acid, through hydrolysis and oxidation, splitting into urea and carbon dioxide



that in reptiles where oxidation is less rapid than in mammals and in birds when any saving of oxidation is of advantage, urea in the urine is replaced by uric acid, that the molecule of uric acid contains the residues of two molecules of urea as shown by the formula expressing its chemical constitution



it has been held that uric acid must be regarded as imperfectly oxidized urea. On the other hand, it is considered by many chemists that uric acid cannot be an antecedent of urea, being formed by a synthesis, possibly of lactic acid and ammonia, in the liver or elsewhere, rather than by the imperfect oxidation of proteid matter. Accord-

[1] British Medical Journal, 1885, p. 1100.

ing to this point of view the relative production of uric acid and urea in different animals depends not upon the extent of oxidation, but on the structure of the uriniferous tubules, the amount of water absorbed, the general physical conditions involved, etc., being better adapted to the excretion of uric acid in one kind of animal and of urea in another. It must be admitted, however, that neither of these explanations offers a satisfactory answer as to why the principal nitrogenous constituent in the urine of reptiles and birds should be uric acid and of mammals urea. In this connection it will be recalled as already mentioned that a number of substances closely allied in chemical constitution to uric acid, such as xanthin, guanin, hypoxanthin, adenin, etc., are found in small quantities in the urine and which constitute when taken together the so-called xanthin group. Allantoin ($C_4H_6N_4O_3$), found in the urine of children within a few days after birth, and in very small quantities in that of the adult in the allantoic fluid (hence its name), is also a derivative of uric acid, being derived by the oxidation of the latter.

Hippuric Acid.—Hippuric acid, or benzoyl-amido acetic acid ($C_9H_9NO_3$), is one of the few important constituents of the urine that is produced in the kidneys themselves, being formed in these organs by the union of benzoic and amido acetic acids (glycin, glycocoll) with dehydration.

Benzoic acid. Glycin. Water. Hippuric acid.

$$C_7H_6O_2 + C_2H_5NO_2 - H_2O = C_9H_9NO_3$$

That such is the origin of hippuric acid within the economy appears from the fact that if arterialized blood containing benzoic acid be passed through the blood vessels of a freshly excised "surviving" dog's kidney, hippuric acid will be found in the perfused blood.

On the other hand, as in jaundiced patients, and in animals in which the liver is extirpated, or the ductus communis is ligated, the benzoic acid administered passes out of the body as such, one would be led to suppose that the synthesis with glycin takes place in the liver.

FIG. 225.

Hippuric acid. (LANDOIS.)

It would appear, therefore, that hippuric acid may be produced by the synthesis just mentioned in different parts of the body, more particularly in the dog in the kidney, in the rabbit in the liver, and in man in one or both organs. As a further confirmation of the synthetic origin of hippuric acid, it may be mentioned that when benzoic acid is taken internally the amount of hip-

puric acid excreted in the urine is increased.[1] It is also well known that a benzoic acid residue exists in the fodder of ruminants, and which accounts in the above supposition for hippuric acid replacing uric acid in the urine of such animals.[2] As hippuric acid is found, however, in the urine of a starving man, or of one upon a meat diet, though in less quantity than when on a vegetable or mixed one, the benzoic acid, like the glycin, must be derived from the disintegration of proteid materials. Hippuric acid (Fig. 225) crystallizes in semi-transparent, four-sided rhombic prisms or columns, or in needles if the crystallization is rapid.

The hippuric acid excreted in the urine during twenty-four hours amounts upon a mixed diet to about 0.7 grammes (10.8 grains). If the food consists, however, of fruit, especially plums, it may then amount to as much as 2 grammes (30 grains).

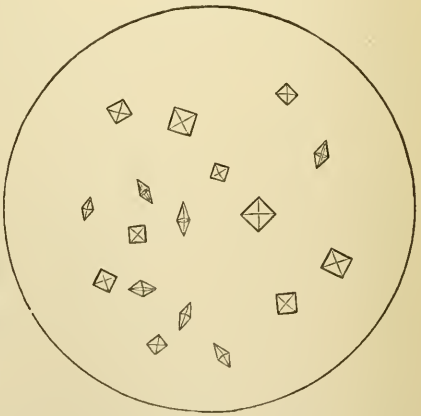
Creatinin.—Creatinin ($C_4H_7N_3O$), regarded as being the anhydride of creatin ($C_4H_9N_3O_2$), appears in the urine in the form of colorless, shining, monoclinic prisms.

The quantity of creatinin excreted in the urine in twenty-four hours amounts on the average to about one gramme. While the amount excreted depends to a great extent upon the quantity of meat eaten, the creatin of the latter being converted into creatinin and eliminated in that form, part is also derived from the proteid of the body, as creatinin is still found in the urine of the starving man even if in diminished amount.

FIG. 226.

Creatinin, crystallized from hot water. (LEHMANN.)

FIG. 227.



Calcium oxalate. Deposited from healthy urine.

Oxalic Acid.—Oxalic acid ($C_2H_2O_4$) occurs in the urine in very small amounts (0.02 gramme (0.3 grain) per day) as calcium oxalate which is kept in solution by the acid sodium phosphate. When deposited in the urine in consequence of ammoniacal fermentation,

[1] Matschersky, Virchow's Archiv, 1863, s. 528.
[2] Meissner and Shepard, Centralblatt, 1866, Nos. 43 and 44.

calcium oxalate crystallizes (Fig. 227) as regular octohedra or double quadrangular pyramids united base to base.

Oxalic acid, as already stated,[1] appears to be derived from the food, cabbage, spinach, asparagus, apples, grapes, etc., containing it. It should be mentioned, however, that, according to Hammarsten,[2] oxalic acid has been found in the urine during starvation, and also upon a diet consisting exclusively of flesh and fat, which if the case shows that it may be derived to some extent, at least, from the tissues.

Conjugate Sulphates.—The phenol ($C_6H_5OSO_3H$) and cresol ($CH_7OSO_3H_7$) sulphuric acids, and indoxyl ($C_8H_7NSO_4$) and skatoxyl ($C_9H_9NSO_4$) sulphuric acids that occur in small quantities as alkaline salts in the urine are derived as already mentioned[3] from the phenol (C_6H_5OH) and cresol (C_7H_7OH) and indol (C_8H_7N) and skatol (C_9H_9N) that are produced in the intestines by the putrefaction of proteids, and which being carried to the liver, the indol and skatol becoming through oxidation indoxyl and skatoxyl, couple with sulphuric

$$\overset{\text{Indol.}}{C_8H_7N} + O = \overset{\text{Indoxyl.}}{C_8H_6(OH)N}$$

acid to form the ethereal or conjugate sulphates and are in that form eliminated by the kidneys. The presence in the urine of potassium indoxyl sulphate, or indican, as it is usually called, can be readily shown by mixing equal volumes of urine and hydrochloric acid and adding two or three drops of a solution of chlorinated lime, whereby oxygen being liberated, the indican is decomposed into indigo blue and potassium acid sulphate.

$$\overset{\text{Indican.}}{2C_8H_6NKSO_4} + O_2 = \overset{\text{Indigo blue.}}{C_{16}H_{10}N_2O_2} + \overset{\text{Potassium acid sulphate.}}{2HKSO_4}$$

By adding chloroform and shaking the mixture vigorously for some time, the blue coloring matter is dissolved, and after the chloroform evaporates remains as a deposit. The amount of indican found in the urine is very small, 0.005–0.02 gr. (0.07–0.3 grains) only being excreted in twenty-four hours. It may be mentioned in this connection, as an interesting fact, that 25 times as much indican occurs in the urine of the horse as in that of man. Aromatic oxyacids, such as paraoxyphenyl acetic acid ($C_6H_4OHC_2H_3O_2$) and paraoxyphenol-propionic acid ($C_6H_4OHC_3H_5O_2$), derived from tyrosin as intermediate steps in the putrefaction of proteids in the intestines, are also found in small quantities in the urine, together with some other organic substances, which have been already referred to in our account of the chemistry of the body.

Inorganic Constituents of the Urine.—Of these, water is the most important, constituting 95.4 per cent. of the whole urine, 1572 grammes of urine containing 1500 grammes of water. The salts of the urine are taken into the body with the food and pass out of

[1] P. 50. [2] Op. cit., p. 357. [3] Pp. 82, 109, 225.

it as such in the urine unchanged, or they are produced within the system through oxidation of the sulphur and phosphorus either of the food or tissue, the sulphuric and phosphoric acids combining with bases to form salts. The amount of salts excreted daily in the urine upon a mixed diet varies from 9 to 25 grammes (139 to 386 grains). It is impossible as yet to state exactly the manner in which the chemical elements are combined with each other or the acids with the bases, since the composition of the ash corresponds almost exactly with the direct analysis of the urine. It is for this reason that the amounts of chlorine and sodium, for example, occurring in the urine are stated separately in an analysis of the latter rather than as combined as sodium chloride. It is very probable, however, that the sodium, and potassium also, occurring in the urine do exist there as chlorides; phosphoric acid in combination with sodium and potassium as alkaline, and with calcium and magnesium as earthy phosphates; sulphuric acid with sodium and potassium as alkaline sulphates; uric acid as sodium urate. With the exception of water, sodium chloride constitutes by far the greatest part of the inorganic principles of the urine, as much as from 10 to 15 grammes (154 to 231 grains) being excreted in twenty-four hours. The amount of sodium chloride occurring in the urine depending almost entirely upon that contained in the food, the chlorine estimated as such will vary therefore proportionally.

The phosphoric acid of the urine is excreted principally in the form of potassium and sodium phosphate. The amount of alkaline phosphates excreted in twenty-four hours (2.6 grammes, 45 grains) varies with the kind of food taken, being greater on an animal than on a vegetable diet, the former being richest in soluble phosphates or substances yielding readily phosphoric acid. The earthy phosphates, calcium and magnesium phosphate, while derived principally from the food, are no doubt formed also within the system through the decomposition of lecithin, nuclein, etc. The earthy phosphates excreted in twenty-four hours amount to about 2.3 grammes (35.5 grains). The alkaline sulphates excreted in the urine amount in twenty-four hours to about 2.5 grammes (40 grains). The sulphuric acid excreted in the urine is derived from the food only to a very small extent, the greatest part being formed within the body by the burning of the tissues. It is for this reason that the total destruction of body proteid can be estimated from the amount of sulphur eliminated in the urine[1] as well as from the nitrogen. The sulphuric acid eliminated is, as regards the nitrogen in the ratio of 1 to 5. Sulphur occurs in the urine not only in the form of sulphates and ethereal sulphates, but also as "neutral sulphur" in which form it is found in cystin and sulphocyanides. In addition to the constituents already mentioned the urine contains

[1] Proteid : sulphur :: 100 : 2.2.

$$\text{Proteid} = S \times \frac{100}{2.2} = 45.4.$$

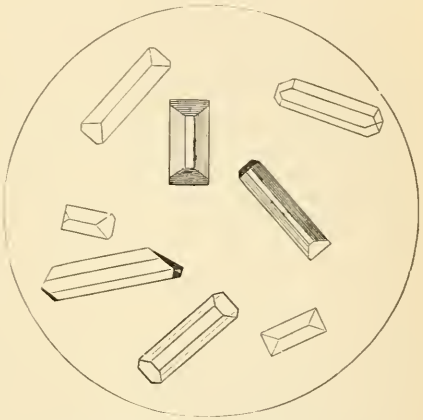
usually traces of nitric and silicic acids, ammonia and iron, carbon dioxide in varying amounts, nitrogen in small quantities (0.8 vol. per cent.) and oxygen in traces.

Fermentation of the Urine.—In concluding our account of the urine, the changes produced in it by standing may be here briefly

FIG. 228.

Micrococcus ureæ. (LANDOIS.)

FIG. 229.



Ammonium magnesium phosphate. Deposited from healthy urine, during alkaline fermentation.

alluded to. It will be remembered that the urine, when first passed, is acid, the acidity being due to the acid sodium phosphate. Within twelve or twenty-four hours, however, through the development of a lactic or acetic acid fermentation, brought about by mucus or fungi, uric acid and acid urates are precipitated, and the urine undergoes the so-called "acid fermentation."

After a few days this acid fermentation ceases, through the conversion of urea by the addition of water into carbonate of ammonium,

Urea. Water. Ammonium carbonate.

$$CON_2H_4 + 2(H_2O) = (NH_4)_2CO_3$$

the changes being brought about by the action of the micrococcus ureæ (Fig. 228).

The acid sodium phosphate being then neutralized by the ammonium carbonate so formed, the urine becomes alkaline.

Acid sodium phos. Ammon. carb. Ammon. sodium phos. Carb. dioxide. Water.

$$2NaH_2PO_4 + (NH_4)_2CO_3 = 2NaNH_4HPO_4 + CO_2 + H_2O$$

With the alkalinity of the urine, the earthy phosphates, being only soluble in acid fluids, are precipitated, and in combining with the ammonia give rise to the formation of the triple phosphate or ammonium magnesium phosphate (Fig. 229).

Magnesium phos. Ammon. carb. Ammon. mag. phos. Carb. dioxide. Water.

$$2MgHPO_4 + (NH_4)_2CO_3 = 2MgNH_4PO_4 + CO_2 + H_2O$$

As decomposition goes on, the ammonium carbonate, after saturating the elements with which it is capable of uniting, is given off free, giving rise to the ammoniacal odor of the urine, and this continues until all of the urea has disappeared.

CHAPTER XXVI.

THE NERVOUS SYSTEM.

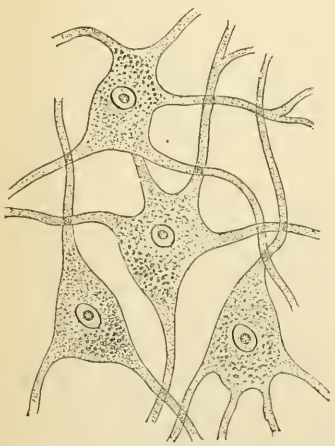
In describing the manner in which food is digested, absorbed, and circulated through the economy as blood, supplying the material for the repair of the tissues and the production of energy, of the absorption of oxygen, and exhalation of carbon dioxide, water, urea, etc., the influence exerted by the nervous system upon these processes has only been alluded to, if at all, in an incidental manner. That the phenomena of nutrition are not dependent upon the nervous system, however much it may be influenced by the latter, is shown from the fact that the nutrition of the lower animals, in which the nervous system is but little developed, and of plants, in which, with but few exceptions, so far as is known, it is altogether absent, does not differ from the higher forms of animal life. Indeed, the essential difference between the nutrition of plants, as compared with animals, consists of the deoxidation by plants of the water, carbon dioxide, and ammonia constituting their food, into starch, sugar, fats, albumin, and the storing up of energy, and the oxidation by animals of the latter substances constituting their food, into carbon dioxide, water, and ammonia, and the expenditure of energy. But while such a broad distinction exists between plants and animals, as compared, on the whole, nevertheless, it must not be lost sight of that oxidations, analytical processes, are going on in the economy of plants incidental to the elaboration and circulation of the sap, the production of heat, in budding, flowering, etc., and deoxidations, synthetical processes in the economy of animals. Indeed, as has already been mentioned, no sharp line of demarcation can be drawn between vegetable and animal life. While nutrition is not actually dependent upon the nervous system, nevertheless every one is, however, conscious of the extent to which it influences nutritive processes. The sudden manner in which digestion is brought to a stop by a piece of bad news, the weakness of the heart induced by nervous shock, the sudden blush or pallor due to emotion, are familiar illustrations. The flow of the secretions into the alimentary canal in response to food, the rhythmical action of the heart and lungs, though unconsciously brought about, are due equally to the action of the nervous system. The influence of the nervous system upon nutrition has often been compared to that exercised by the rider upon the movements of a horse, the energy being put forth by the latter, but controlled with bit and spur by the former. Man, like other animals, is, however, something more than a mere nutritive machine, becoming conscious, through

his nervous system, of an external world. Impressions made upon afferent nerves by heat, light, sound, etc., when conveyed to the sensorium, give rise there to sensations, out of which are developed in still higher centers, emotions, desires, ideas, while voluntary impulses are transmitted in the reverse direction by efferent nerves to the muscles. In a word, it is by means of the nervous system that the various nutritive processes that we have studied are brought into relation with each other—are coördinated—that we feel, think, will.

Structure of the Nervous System.

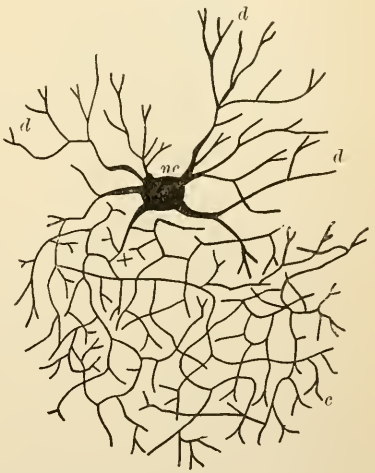
The nervous system consists morphologically of an association of numerous and independent neurons, that is, of nerve cells and their outgrowths. The nerve cells are confined in a great measure to the cerebro-spinal axis and ganglia; the outgrowths are found, however, throughout the body. Nerve cells (Fig. 230) are nucle-

FIG. 230.



Nerve cells, from the anterior horn of gray substance of the spinal cord.

FIG. 231.

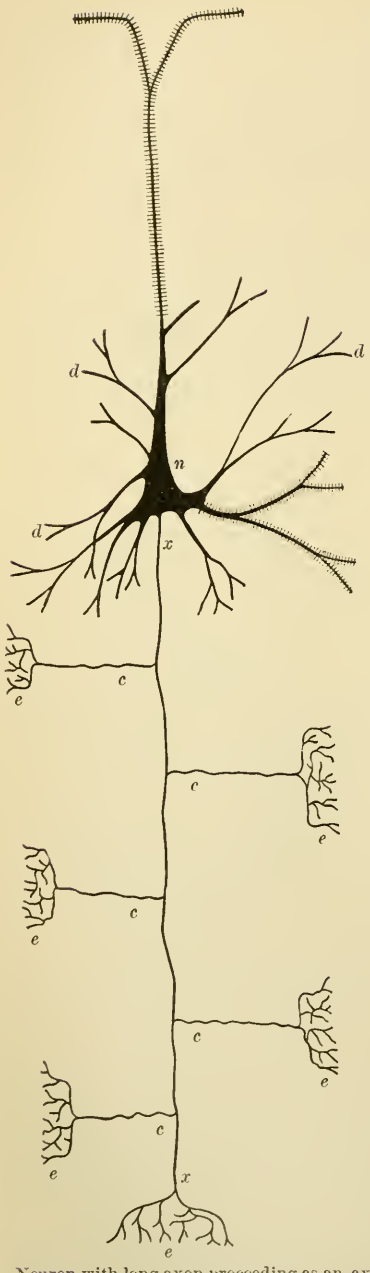


Neuron with short axon immediately breaking up into numerous fine filaments. *n c.* Nerve-cell proper. *x.* Axon. *d.* Dendrites. From the cerebellum. (ANDRIEZEN.)

ated cells usually more or less ovoid in shape, and differ considerably in size, varying in diameter from the $\frac{1}{100}$ to the $\frac{1}{8}$ of a millimeter ($\frac{1}{2500}$ to $\frac{1}{200}$ of an inch). According to recent researches[1] a nerve cell appears to consist of a kind of framework, continuous with the fibrillæ of the nerve fiber, in the meshes of which are contained small masses or granules readily stainable with basic aniline dye. Nerve cells occur not only separately, but in many cases are aggregated together as ganglia. The latter are generally provided with a thin but strong and closely adherent capsule or sheath continuous with the epineurium or supporting framework of the nerve fibers.

[1] Nissl, Allgemein Zeits für Psychiatrie, Band 52, 1896, s. 1147.

Fig. 232.



Neuron with long axon proceeding as an axis cylinder of a nerve fiber. *n c.* Nerve-cell proper. *d.* Dendrites. *x.* Axon. *d g.* Dendrite showing gemmulæ. *a d g.* Apical dendrite with gemmulæ. *c.* Collaterals. *e.* End tufts. Pyramidal cell of the cerebral cortex. (S. Ramón y Cajal.)

From most nerve cells, in mammals at least, there arises one principal branch or process, the axon. Such cells are called, therefore, monaxonic. In some of the lower animals, however, the nerve cells giving rise to two or more axons are therefore diaxonic and polyaxonic. The axons differ very much in length, those of the cerebellum (Fig. 231), being less than a millimeter, those of the pyramidal cells of the cerebral cortex (Fig. 232, *x*) as much as 60 cent. (24 inches) long. Indeed, the axons extending from the lumbar region of the cord to the feet attain a length of 100 cent. (40 inches). The volume of the axons in reference to the cells of which they are the outgrowths is also very variable. Thus, while the volume of the axon in the cerebral cortex has been estimated as being 220 times that of the cell, the volume of the axon in the lumbar portion of the cord may be 1570 times as great. In most cases the axons give off both near their origin and throughout their course collateral branches (Figs. 231, 232 *c*), the so-called paraxons, fine filamentous processes which leave the parent branch at right angles and terminate in end tufts (Fig. 232). The axon itself terminates always in a free extremity. The latter may consist of a free undivided filament, but more usually splits up into a number of very fine filaments or end tufts (Fig. 232) similar to those terminating the paraxons.

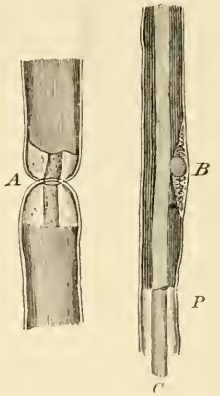
From nerve cells there arise not only axons but other out-

growths, which, dividing dichotomously, present a tree-like appearance; hence the name of dendrites or dendrons (Figs. 231 and

Fig. 233.

Ontogenetic development of a neuron (pyramidal cell of the cerebral cortex) in a typical mammal. *a*. Neuroblast with primitive axon (*ax*) and without dendrons (dendrites). *b*. Commencing dendrons. *c*. Dendrons further developed. *d*. First appearance of collaterals. *e*. Further development of collaterals and dendrons. (S. Ramón y Cajal.)

Fig. 234.



Medulated nerve fiber. *A*. Node of Ranvier. *B*. Nucleus belonging to the neurilemma. *C*. Axis-cylinder. *P*. Neurilemma rendered distinct by the retraction of the myelin of the medullary sheath. In the left-hand figure the clefts of Lantermann are shown as white lines in the dark myelin. The figures are taken from specimens treated with osmic acid, which colors the fatty constituent of the myelin a dark brown or black. (Key and Retzius.)

232, *d*) by which they are usually designated. The dendrons, while described as outgrowths or processes of the nerve cell, should rather be regarded morphologically as the split-up portion of its periphery than as differentiated processes like the axons. In many instances there arise from the dendrons short rectangular or oblique, lateral projections or buds, the so-called gemmulæ (Fig. 232), etc. The nerve cells with their outgrowths are derived from the spherical cells which appear during the third or fourth month of intrauterine life[1] among the columnar epiblastic cells which form the primitive medullary tube. These cells divide in such a way that of two daughter cells resulting from division, while one remains as a germinal cell the other becomes a neuroblast and moves away. It is an interesting fact that the power of moving possessed by the nerve cells at this early period of their existence appears, from recent researches,[2] to be retained, to some extent at least, throughout life. The neuroblasts so produced soon lose their spherical shape and become pyriform.[3] In the mean-

[1] His, Du Bois Reymond's Archiv, 1889.

[2] F. X. Dercum, Univ. Medical Magazine, April, 1897.

[3] Ramón y Cajal, El nuevo concepto de la histologia de los centros nerviosos, Revista De Ciencias De Barcelona, Tomo xviii., 1892, pp. 361–457.

time a protuberance appears at one point of the periphery of what may be now called the nerve cell, and which, gradually elongating, becomes the primitive axon (Fig. 233, *ax*), while from the opposite pole of the cell arise the dendrons. With the assumption of the nerve cell of its typical form and the production of chromatic and pigmentary materials, etc., its branches grow, increasing in length and diameter, the axon being gradually converted into a naked, gray axis-cylinder (Fig. 234), or that portion of the ultimate nerve fiber which conveys the nervous impulse from the brain and cord to the periphery or in the reverse direction.[1] Difference of opinion still prevails among histologists as to the structure of the axis-cylinder, according to some [2] it being composed of slender fibrillæ floating in a coagulable plasma, to others [3] of a spongy framework, in the meshes of which is a semi-fluid plasma, the nervous impulse being transmitted through the fibrillæ, according to the one view, and through the plasma, according to the other. The axis-cylinder appears to be chemically of an albuminous nature, insoluble in water, alcohol, and ether, but soluble in a boiling solution of sodium hydrate. As development advances the naked, gray axis-cylinders, or fibers (Fig. 234, *C*), become invested in the brain and spinal cord, except at their origin and termination, with a white medullary sheath, the myelin, or so-called white substance of Schwann (Fig. 234), a transparent, highly refractive oleaginous material, and to which the white glistening aspect of the nerve fiber is due. In the case of the peripheral nerves the white substance of Schwann becomes covered in turn by a membranous sheath, the neurilemma, tubular membrane, or sheath of Schwann (Fig. 234, *P*), a colorless, transparent, somewhat elastic, almost homogeneous membrane, the neurilemma, bears to the nerve fiber in its general properties very much the same relation that sarcolemma does to muscular fiber, and serves, without doubt, as a protective covering to the white substance of Schwann, and the axis-cylinder enclosed by the former. At regular intervals, along the neurilemma, may be observed indentations, the so-called constrictions, or nodes of Ranvier (Fig. 234, *A*). At these nodes the white substance of Schwann, or medullary sheath, is indented to such an extent that the neurilemma, or sheath of Schwann, comes in contact with the axis-cylinder, the spaces outside the neurilemma being filled in with a cement-like substance. From the fact that a substance like picro-carmine diffuses into the axis-cylinder only at the nodes, but not into the whole substance, it is possible

[1] Since the above was written there has appeared an article by Apathy (Mittheil aus der zoo Station, zu Neapel, V. 12, 1897), in which it is held that while the nerve cell produces neuro-fibrils, the ganglion cell produces the force which is to be conducted, the neuro-fibrils traversing the ganglion cells and terminating in or around a muscle or sense cell. According to the same author the cell process of a ganglion cell not only contains both cellulipetal (centripetal) and cellulifugal (centrifugal) fibers, but the nerve processes anastomose. If these views be substantiated the conception of a neuron will have to be modified or even abandoned.

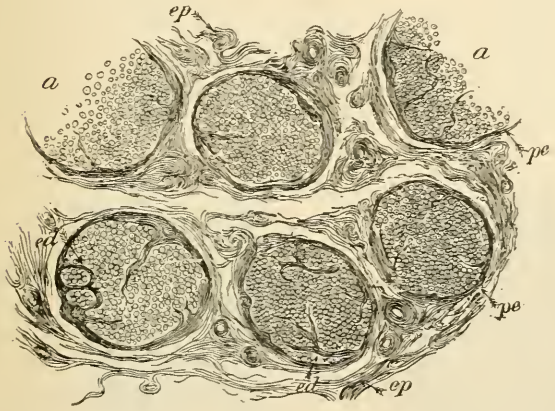
[2] Kuppfer u. Boveri, Abhandl. d. k. bayer. Akad. d. Wissen., 1885.

[3] Schäfer, Quain's Anatomy, 10th edition, Vol. i., 1891.

that it is at such points that nutritive material finds its way into the axis-cylinder and effete matter a way out. Each interannular segment of that part of the nerve fiber below the nodes exhibits, when stretched, oblique lines running across the white substance, and known as the incissures of Lantermann. Oval nuclei (Fig. 234, *B*) may also be seen at intervals between the neurilemma and the white substance of Schwann.

The aggregation of medullary nerve fibers such as those just described into bundles and the further union of such bundles into larger ones give rise to the peripheral nerves, the ultimate nerve fibers of the latter being separated from each other by the endoneurium (Fig. 235, *ed*), each bundle of nerve fibers being sur-

FIG. 235.



Transverse section of part of the median nerve. *ep*. Epineurium. *pe*. Perineurium. *ed*. Endoneurium. (After EICHHORST.) *a*, *a*. Funiculus. (LANDOIS.)

FIG. 236.

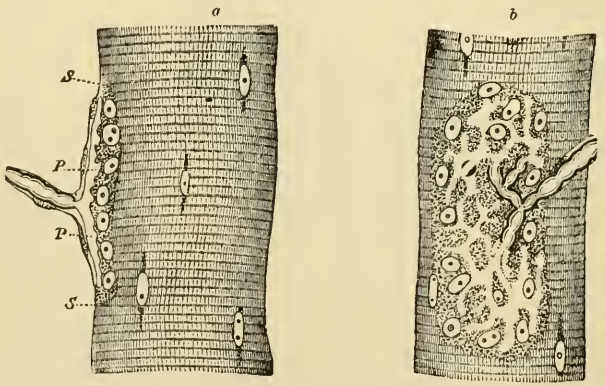
Fibers of Remak; magnified 300 diameters. With the gelatinous fibers are seen two of the ordinary, dark bordered nerve fibers. (ROBIN.)

rounded by its perineurium *pe*, and the bundles or funiculi being supported by the perineurium. The axis-cylinders that occur, however, largely in the sympathetic and to some extent also in the cerebro-spinal nerves differ from those just described in not being invested with a medulla, though covered with a neurilemma, or membranous sheath. The non-medullated, gelatinous nerve fibers, or fibers of Remak (Fig. 236) as they are often called, are pale, flattened, gray, granular fibers presenting well-marked oval nuclei. It is impossible to say at present whether the non-medullated nerve fibers have different functions from those of the medullated ones, or to assign any definite function to the medulla when present. From the fact that the axis-cylinder is the only constant portion of the ultimate nerve fiber, the intermediate white substance and external sheath being absent at the origin and termination of the latter, there can be no doubt that it is the most important, indeed, the

essential, portion, functionally, of the nerve fiber, the remaining portions having accessory functions no doubt of some kind. Inasmuch as up to the fifth month of intrauterine life the nerves generally have essentially the same structure as the so-called gelatinous fibers of the adult, and as during the regeneration of nerves after injury or division the new elements pass in their development through a transitory stage comparable in structure to that of the gelatinous fibers, the latter may be regarded perhaps, morphologically, as undeveloped medullated or non-medullated fibers.

If the nerve fibers be traced from their origin in the nerve cells of the cerebro-spinal axis to their termination in muscles, glands of the periphery, or in the reverse direction from the sensory organs to their termination in the cells of the cord and brain, it will be observed as already mentioned that the only part of the ultimate nerve fiber found at either origin or termination is the axis-cylinder. Thus in the termination of nerve fibers in muscles where the axis-cylinder passes into the latter, expanding into the motor plate (Fig. 237), the neurilemma of the nerve fibers becomes con-

FIG. 237.



Nerve-ending in muscular fiber of a lizard. (Lacerta viridis.) *a*. End-plate seen edgeways. *b*. From the surface. *S, S*. Sarcolemma. *P*, ‖*P*. Expansion of axis-cylinder. In *b* the expansion of the axis-cylinder appears as a clear network branching from the divisions of the medullated fiber. Highly magnified. (KUHNE.)

tinuous with the sarcolemma of the muscle, while the white substance of Schwann, though continuing to the muscle, does not, however, penetrate into it, and while there may be still doubt prevailing as to whether the axis-cylinder passes into the nuclei of the cells of a gland in the manner supposed to be the case by Pflüger and others, in the salivary gland, for example, there is no doubt that, however exactly the axis-cylinder does terminate in glands, it is the only part of the nerve fiber that actually reaches the cells, of which such organs consist. Such is essentially, also, the disposition that obtains in the case of sensory organs, so far as has been established. Thus, whether it be a Pacinian corpuscle attached to

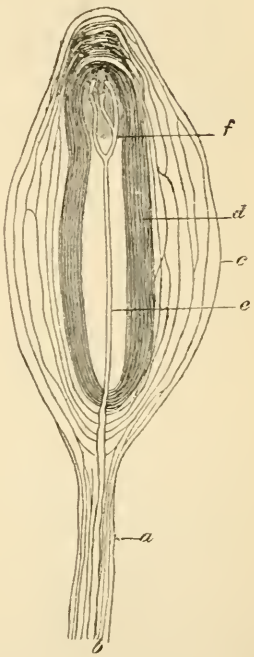
sensory nerves (Fig. 238, A, B), or a tactile corpuscle (Fig. 239), as we shall see, are present in the skin, or an end bulb (Fig. 240)

FIG. 238.

A

A nerve of the middle finger, with Pacinian bodies attached. Natural size. (HENLE and KOLLIKER.)

B

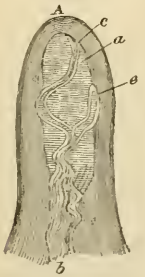


Vater's or Pacini's corpuscle. *a*. Stalk. *b*. Nerve fiber entering it. *a*, *d*. Connective tissue envelope. *c*. Axis-cylinder, with its end provided at *f*. (QUAIN.)

such as is found in the conjunctiva; in each instance the neurilemma of the nerve fiber becomes continuous with the capsule enclosing such bodies, the white substance of Schwann remains without the latter, the axis-cylinder alone penetrating within.

Experimental investigation, as well as morphological considerations, proves that the axis-cylinders of the nerve fibers are the avenues by which nervous impulses emanating from the cells of the

FIG. 239.



a. Tactile corpuscle. *b*. Nerve. (QUAIN.)

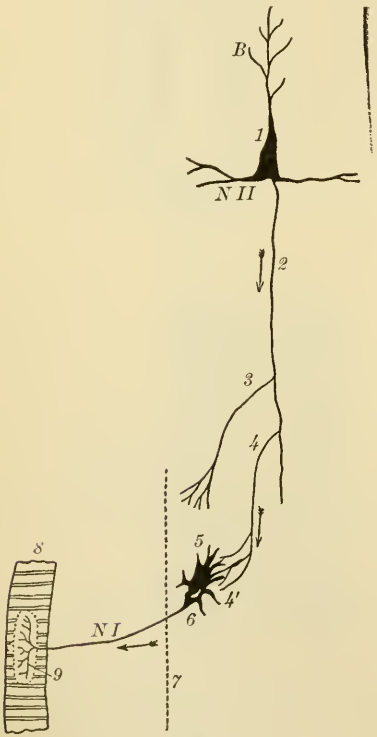
FIG. 240.

Three nerve-end bulbs from the human conjunctiva, treated with acetic acid. Magnified 300 diameters. (QUAIN.)

brain and cord are transmitted as efferent impulses to muscles, glands, etc., and by which impressions made upon the skin, sensory

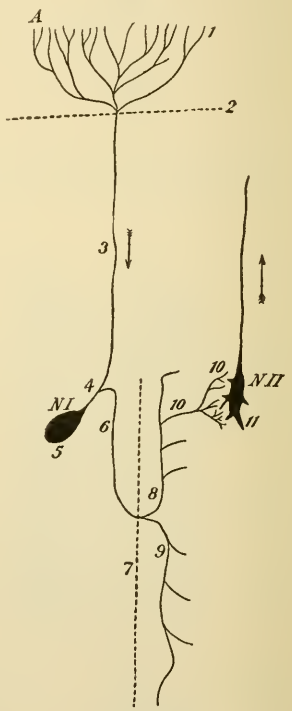
organs are transmitted as afferent ones to the cells of the cord and brain. As the neurons of which the nervous system is composed are, however, entirely independent of each other, never absolutely continuous, it must be admitted that even though a nervous impulse may pass continuously from the cerebral cortex (Fig. 241, *I*) to the lumbar enlargement of the cord 4′ that arriving there it must pass over a gap, 4′ to 5, in order to reach the next neuron, *N I*, that will in turn carry it on to the foot. Or let us suppose that an impression made upon the skin (Fig. 242, 1) is transmitted

Fig. 241.



Diagrammatic representation of cerebral and spinal motor cells with axons. 1. Cerebral cell. 2. Axon. 3, 4. Collaterals. 4′. End tufts. 5. Spinal cell. 6. Axon. 7. Limit of spinal cord. *NI*. Motor nerve. 8. Muscle. 9. Muscle-end plate. (Rauber.)

Fig. 242.



Diagrammatic representation of cerebral and spinal sensory cells with axons. 1. Skin end tufts. 2. Limit of epidermis. 3. Axon. 4. Common stem. 5. Cell in spinal ganglion. 6. Axon. 7. Limit of spinal cord. 8. Ascending branch. 9. Descending branch. 10. End tufts. 11. Spinal cell. 12. Axon. (Rauber.)

continuously to a cell 5 in a spinal ganglion and thence to 10; on arriving at the latter point it must pass over a gap in order to reach the next neuron, *N II*.[1] It will be observed that there arises from the cell 5 (Fig. 242) in the spinal ganglion one outgrowth or nerve fiber that conducts in two directions towards the nerve cell and away from it, presenting apparently an exceptional disposition to that already described. The study of development shows, how-

[1] A. Rauber, Lehrbuch Der Anatomie Des Menschen, Zweiter Band, 1898, s. 270.

ever, that such a nerve fiber consists really of two fibers, afferent and efferent, which have become so closely associated that their original identity is lost. Such cells do not differ, therefore, functionally from those in which the outgrowths are situated at different points of the cell. Various explanations have been offered as to how the nervous impulse in the first neuron sets up an impulse in the second one. It has been urged that the neurons may extend their outgrowths until they come in contact temporarily with each other, or that the secondary nervous impulse is developed through a process of induction—or that the tips of the nerve fibrils cause some chemical change in the intervening substance which gives rise to the secondary impulse. It must be admitted, however, that these so-called explanations are merely hypotheses, and that the manner in which nervous impulses are transmitted from neuron to neuron is not as yet understood. Nerve cells, like all cells, have a life history, and as recent researches[1] show, in old age the chromatic substance of the cells diminish while the pigment increases, the cytoplasm becomes vacuolated, the outgrowths atrophy, and in some instances the entire cell is absorbed.

Chemical Composition of the Nervous Tissues.—Less is known of the composition of the nervous tissues than of any other tissues of the body. They appear, however, like the tissues in general, to be composed largely of water, which enters into the constitution of the white matter to the extent of 70 per cent. and into that of the gray to about 75 per cent. Among the solid constituents of the nervous tissues the most important are insoluble albumin and connective tissue, protagon, cholesterin, neurokeratin, nuclein, and mineral bodies.[2] Of these substances albumin and connective tissue occur in greater quantity in the gray matter than in the white, the remaining ones, however, in greater quantity in the white than in the gray. Protagon ($C_{160}H_{308}N_5PO_{35}$), a crystalline substance, consists, according to most chemists, of lecithin and cerebrin. Lecithin appears, as already mentioned,[3] to be a triatomic alcohol readily breaking up into fatty acids, glycero-phosphoric acids, and cholin, the latter giving rise to neurin. Cerebrin resembles lecithin in being a nitrogenous substance, but differs from the latter in not containing phosphorus; it appears to be a glucoside yielding that form of sugar known as galactose. The cholesterin found in the nervous tissues occurs partly free and partly in chemical combination. Neurokeratin is found in the peripheral nerves as a delicate sheath covering the axis-cylinder and white substance of Schwann. Nuclein, or the substance of which the nucleus of the nerve cell is composed, appears to be a phosphorized albuminoid. The mineral bodies occurring in the nervous tissues consist of the salts of potassium, sodium, magnesium, calcium, and iron. Extractives, such as creatin, xanthin, hypoxanthin, moist lactic acid, leucin, uric acid, and urea are found in small quantities.

[1] Hodge, Journal of Physiology, Vol. xvii., 1894.
[2] Hammarsten, op. cit., p. 279. [3] See p. 66.

CHAPTER XXVII.

THE NERVOUS SYSTEM.—(*Continued.*)

BATTERIES. OHM'S LAW. INDUCTION APPARATUS. PENDULUM MYOGRAPH. LATENT PERIOD. VELOCITY OF CONDUCTION OF NERVOUS IMPULSE.

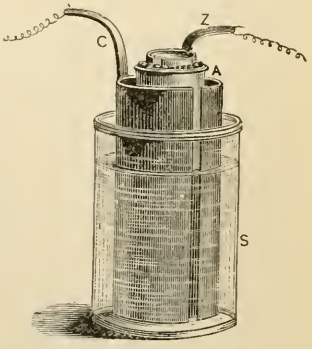
From daily observation we learn that all our actions are the result of motives or stimuli. Impressions made upon the surface of the body and transmitted by nerves to the central nervous system and there giving rise to sensations, are immediately or mediately followed by actions. The impressions made may be so strong, and the corresponding sensation arising so acute, that action instantly follows, as in the sudden involuntary shrinking from a source of pain, or the sensation giving rise to an idea, a longer or shorter time may intervene, during which period the mind has time to reflect as to the course of action, the individual being swayed by this or that idea or motive, the will being so to speak in abeyance.

Sooner or later, however, one motive becoming the strongest, voluntary action follows, or, to speak in ordinary language, the will asserts itself, the term will being simply a convenient one, for expressing the fact that action is the result of the strongest motive, the result of the preceding stimulus. The sole difference between these two actions, the involuntary and voluntary, is in the interval of time elapsing between the application of the stimulus and the resulting action, and in the stimulus being some external exciting cause other than that of the will, as in the case of a cough, due to a crumb of bread in the larynx, rather than to volition.

In addition, however, to the sensations, or ideas, arising within us due to the stimulation of nerves from without inward and of the involuntary or voluntary actions following due to the reflection of the impulses from such stimulation from within outward of which we are all conscious, there are similar actions following the stimulation of nerves, of which as long as we are in a state of health we are entirely unconscious. As illustrations of such actions may be mentioned the flow of the gastric juice in response to the stimulus exerted by food upon the nerves distributed to the stomach, of the dilatation or contraction of the blood vessels brought about through the influence of nervous emotion, of the contraction of the iris in response to light. The phenomena of secretion, like those of sensation, involuntary and voluntary movements, result from the application of a stimulus to peripheral nerves, which, being transmitted to the nervous centers, is thence reflected to the parts manifesting

the phenomena. That it is by means of the nerves connecting the periphery with the nervous center, and the center with the organs manifesting the phenomena, that the latter are produced becomes at once evident if the nerves involved be destroyed, whether by disease, injury, or experiment; sensation, voluntary movement, secretion, etc., at once disappearing. The involuntary muscular contraction, the result of pain, the voluntary one made in the carrying out of some matured plan, and the flow of a secretion, are equally illustrations of the truth of all nervous action being of this reflex character. In every instance if the phenomenon be traced to its source it will become evident that an action apparently due to an impulse generated from within and transmitted outward is in reality due to an impression first made from without and transmitted inward, and then finally reflected outward. That nervous energy, whatever its nature may be, is never generated spontaneously, but must be of this reflex character, some modified prëexistent mode of energy, is self-evident, otherwise nerve energy would arise out of nothing. Whatever view may be taken, however, of the origin of ideas, the nature of the will, etc., it will not affect the fact that the irritability of nerves, like that of other tissues, may be called into excitement by appropriate stimuli. While the irritability of a muscle, however, shows itself by its contraction, and that of a gland by its secretion, that of the nerve is not manifested by any ordinary visible change in itself, but by some change in the organ to which it is distributed.[1] Of the different stimuli, mechanical, chemical, and electrical, available in calling into excitement the property of irritability possessed by nerves, the electrical is by far the most convenient, and since the contraction of a muscle brought about indirectly by the stimulation of the nerve supplying it, is a very striking phenomenon, the muscular contraction may be taken as an evidence and measure of the nervous irritability causing it.

FIG. 243.



Daniell's element. (GANOT.)

As in the stimulation of nerves we shall usually make use of the electricity supplied by a Daniell element, a brief description of the same does not appear superfluous. A single Daniell's element consists (Fig. 243) of a glass vessel S, containing a saturated solution of copper sulphate, in which is immersed a copper cylinder (A), open at both ends and perforated with holes, and provided with an annular shelf supporting crystals of copper sulphate to replace the solution of the same decom-

[1] We shall see presently that the nerve does undergo a change in its electrical condition when excited, but which can only be detected by means of a delicate galvanometer, and that possibly heat is also produced.

posed during the action of the battery. Within the copper cylinder is a thin porous vessel of unglazed earthenware, containing diluted sulphuric acid, in which is placed a cylinder of amalgamated zinc Z. The positive electricity generated by the action of the acid upon the zinc, passing through the liquid of the battery to the copper cylinder, accumulates at the end of the wire attached by the binding screw to the latter (C), the wire becomes, therefore, the positive pole or electrode, though the copper, to which it is attached, from being relatively little acted upon, is called the negative or collecting plate; on the other hand, through the disturbance of the electrical equilibrium the negative electricity developed, passing in the reverse direction from the copper to the zinc, accumulates at the end of the wire attached to the latter (Z), that wire becomes, therefore, the negative pole or electrode; the zinc, however, from being most acted upon, is called the positive or generating plate. As, however, the effect of the battery is due to the difference of electric potential set up between the metals, the current is rather regarded as being single and as flowing from the zinc or positive plate through the liquid of the cell to the copper or negative one, thence by the positive pole through the connecting wire to the negative pole and so back to the zinc plate. Such being the disposition and action of the parts of a Daniell's element when closed, the hydrogen developed by the action of the dilute acid upon the zinc would be deposited upon the copper plate were it not for the presence of the copper sulphate, which the hydrogen reduces into copper and sulphuric acid, the former being deposited upon the copper plate, and the latter replacing that in the porous cup used up in acting upon the zinc; the constancy of the battery is thus insured for several hours at least, upon which its usefulness for our purpose depends. Did the hydrogen gas generated settle in minute bubbles upon the copper plate, which it otherwise would do in the absence of the solution of copper sulphate, the action of the battery would be interfered with by the polarization of the plate, by which is meant that the hydrogen when so deposited not only offers a resistance to the current passing from the zinc to the copper, but in generating a counter current in opposition to the latter proportionately weakens it. It need hardly be added that if two or more Daniell elements are used, in coupling, the zinc plate of one element must be connected with the copper plate of the other by means of a copper wire or stop as in Fig. 245. Among the other forms of batteries often used for physiological purposes may be mentioned those of Bunsen, Smee, Grenet, Leclanché—differing only from the Daniell battery in the character of the metal and liquid used, and their relative arrangement. In describing the action of a Daniell element the electricity generated was spoken of as if flowing through the battery to the poles, as one might speak of the flow of water through pipes, just as if there was an actual electrical current present. As a matter of fact, it is needless to say with refer-

ence to the transmission of electricity, there is no evidence of a transference of particles from place to place as is the case of the flow of water. It will be found, nevertheless, since the molecular changes incidental to the production of electricity are yet unknown, that such a comparison offers an extremely convenient way of presenting the essential facts, of representing to the mind in a connected way results brought about by changes, the intimate nature of which we know nothing. It might be supposed, at first sight, that the consideration of this subject belongs rather to the domain of physics than to physiology; as we shall soon learn, however, that the physiologist not only continually uses electricity as a nerve stimulus, but that both nerve and muscle exhibit electrical currents, and offer a resistance to the passage of electricity, etc., it becomes indispensable that a brief account of the principal facts of electricity be offered, sufficient at least to enable the student to understand the terms constantly used in the description of the phenomena of general nerve physiology.

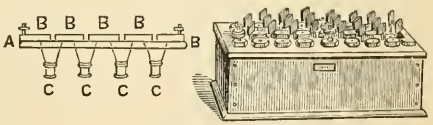
It is a well-established fact that when two metals are placed in contact, as, for example, zinc with copper or platinum, a disturbance in their electrical condition, or, as it is called by physicists, a difference in potential, ensues, the word potential being used in electrical science in the same sense as level or head of water in hydrodynamics. Now just as water at a higher level, if it finds a channel, tends to fall to a lower one until equilibrium is established, similarly if two bodies, or two parts of the same body, have a different potential—that is, are at different electrical levels, so to speak—there will be a tendency to movement from the body having a higher potential to the one with the lower until electrical equilibrium is established. The agent to which this change, movement, so-called electrical current, is due, is called the electromotive force, and while its nature is unknown, it can be measured by the amount of work performed in the passage of a unit of electricity from one position to another, just as the potential energy of water can be measured by the amount of work performed, as in the turning of a water-wheel, etc. Just as the energy exerted in a definite time in raising a weight against gravity may be stored up indefinitely, to be set free again by the falling of the weight, and applied to the performance of mechanical work, so the energy expended in bringing up a body against another similarly electrified, and therefore offering a resistance like that of gravity, may be temporarily stored up, and with the setting free of the electricity perform work. While, therefore, the principle of electrical measurement must be the same as that of other measurements, the particular standards used will not only differ according as statical or dynamical electricity is being considered, but as to what shall be accepted as constituting the unit of time, mass, distance, etc. As a matter of fact, with reference to statical electricity, each of two equally charged bodies is said to have a unit of electricity, if when separated by a dis-

tance of one centimeter the one will repel the other with a force which will impart in one second a velocity of one centimeter per second to one gramme of matter. As regards the galvanic or current electricity with which we have, however, more particularly at this moment to do, the unit of electricity is usually accepted as being that quantity of electricity carried in one second by a current of unit strength. The latter, however, is of course arbitrary, but in the sense just used is one such that if a conductor one centimeter long be bent into an arc of one centimeter radius it will exert a force of one dyne, on a unit magnet pole placed at the center. This is called the electro-magnetic unit of current. For convenience' sake, however, in practice a hundred millions of such absolute electro-magnetic units are taken as a unit constituting the so-called volt, and we speak, therefore, of the electro-motive force of a Daniell's cell being equal to 1.079 volts. Furthermore, the electro-magnetic unit of electro-motive force is that which sends a current of unit strength through a unit resistance, and, therefore, a unit quantity in a unit time, and this definition brings us now to a consideration of the resistance offered by the conductors in the passage of the electricity and the fixing of some standard for the same.

As the unit of resistance must be, of course, an entirely arbitrary one, the standard of resistance ultimately accepted will depend upon what is considered most convenient by physicists. As a matter of fact, at the present time, the resistance offered by a column of mercury about 106 cm. long, and 1 square mm. in section at 0° C., is accepted as the unit of resistance commonly known as the international unit, or one ohm; or, what is the same thing, the resistance offered by a wire made of an alloy of silver and platinum of definite length and thickness, offering the same resistance as the column of mercury just referred to, is accepted as the unit of resistance, or one ohm. The resistance offered by different bodies to the passage of an electrical current varies very considerably, according to the nature of the body. Metals, being the best conductors, offer the least resistance; liquids, especially those of a saline character, conduct, but not so readily as metals. Apart, however, from the conductibility of a particular substance, which is constant for that substance, the resistance offered by a conductor is directly proportional to its length, and inversely proportional to its cross-section—that is, the longer the conductor the greater the resistance, the thicker the conductor the less the resistance. In the case of a galvanic element, however, like that of a Daniell's cell, not only must the resistance offered by the conducting wires, which may be called the external resistance, be taken into consideration, but also the resistance offered by the plates and liquid within the cell, and which may be called the internal resistance. The latter is directly proportional to the distance of the plates from each other, and inversely proportional to the size of the plates—that is, the larger the plates the less the resistance, the conducting power of the liquid, of

course, being assumed to be constant. In the determination of the electro-motive force, resistance, etc., of nerves it will be found, as we shall see presently, that it is of great advantage to vary by known amounts the resistance offered to the passage of an electrical current. For this purpose we make use of a resistance box, which consists, essentially (Fig. 244), of a series of bobbins (C C) on which are coiled various lengths of standard insulated wire, the latter being so disposed in the box that two ends of the wire of each bobbin (C C) are connected with two brass plates (B B) fitted into the lid of the box, the resistance offered by each coil of wire being indicated in ohms on the lid of the box. Suppose, by means of the two binding screws attached to the lid of the box, a current of electricity be sent through the coils C C, the resistance encountered will be equal to the total resistance offered by the coils. If, however, the space intervening between the brass plates be plugged up by tight-fitting brass plugs (Fig. 244), so that the brass plates are then connected, the current will take the route of least resistance, passing simply through the brass portion of the lid of the box, from binding screw to binding screw, without traversing the coils at all. It is obvious, therefore, that the amount of resistance offered to the current passing through the resistance box will depend upon the number of brass plugs taken out. We have just seen that the passage of an electrical current through a galvanic circuit is due to the electro-motive force developed by the element; and further, that, according to the nature of the circuit, the current meets with more or less resistance. It follows, therefore, as shown by Ohm,[1] first from theoretical considerations, and subsequently by experiment, that the strength of the current—that is, the quantity of electricity which, in a unit of time, flows through a given section of the circuit—must be equal to the ratio of the resistance to the electro-motive force. This important result, usually known now as Ohm's law, may be conveniently expressed by the equation $I = \frac{E}{R}$ (1), in which I represents the current strength, E the electro-motive force, and R the resistance.

FIG. 244.



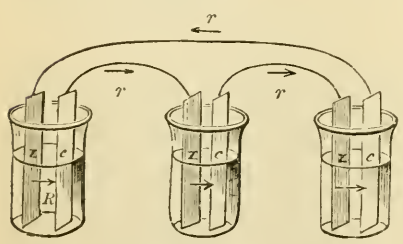
Resistance box.

If in equation (1) E, or the electro-motive force, is equal to 1 volt, and R, or the resistance, to 1 ohm, then I, or the current strength, will be equal to 1 ampère, and the quantity of electricity delivered per second, 1 coulomb, or per hour, 3600 coulombs (hour ampère). As Ohm's law is a most important one, galvanic batteries being arranged by its means so as to give the greatest amount of electricity possible, we will illustrate its application in this respect by a few examples.

[1] Die galvanische Kette mathematisch bearbeitet, Berlin, 1827.

It will be remembered that the resistance of a conductor is directly proportional to its length, and inversely proportional to its conductivity and section. If now the length, conductivity, and section be represented respectively by l, c, and s, then the resistance R will be equal to $\frac{l}{c \times s}$. This value of R being substituted in equation (1) we shall obtain $I = \frac{E}{\frac{l}{cs}} = \frac{csE}{l}$ (2)—that is to say, the intensity of a current is directly proportional to the section and conductivity of the conductor, but inversely proportional to its length. In the case of a galvanic element, as we have seen, the resistance to be considered is not only that of the conducting wires, but also that of the liquid and plates of the element itself. Calling the external resistance, that of the wires, r, and the internal resistance, that of the element, R, we obtain from equation (1) $I = \frac{E}{R + r}$ (3). Now it is obvious that if any number of similar elements are joined together, say three, as in Fig. 245, there is n times the electro-motive force, but, at the same time, n times the internal resistance, and equation (3) becomes $I = \frac{nE}{nR + r}$ (4). If, however, the conducting wires be of copper, and short and thick, then the external resistance r, in comparison with R, may be neglected, and equation (4) becomes $I = \frac{nE}{nR} = \frac{E}{R}$ (5)—that is to say, when the internal resistance is great and the external is small, a battery consisting of several elements—three, in this instance—produces no greater effect than one element. Suppose, on the other hand, that the conducting wires be very long and thin and the external resistance r, therefore, very great, so much so that the internal resistance R can be neglected in comparison; then $I = \frac{nE}{nR + r}$ (4) will become $I = \frac{nE}{r}$ (6), or as $I = \frac{E}{r}$ $I = nI$ (7). That is to say, when the external resistance is large, and internal resistance small, the intensity within certain limits is very nearly proportional to the number of elements—that is, a battery consisting of three elements produces nearly three times the effect of one element. Instead of increasing the number of elements, let us now enlarge the plates, say n, or three times that of a single element (Fig. 246), or join

FIG. 245.



Galvanic battery.

all the copper plates and all the zinc plates together, as in multiple arc and consider what effect will be obtained according to Ohm's law. The electro-motive force under these circumstances, will, of course, remain unchanged—that is, not increased, since it depends upon the nature of the plates and the liquid, and not upon the size of the element, just as the head or force of the water comparable to the electro-motive force is not increased as long as the level remains unchanged, however much the amount of water may be increased, for though there are n times as many regions, in this case—three, where the electro-motive force acts side by side—they do not assist one another any more than the neighboring vertical columns of water in a reservoir affect the pressure on the exit pipe. Nevertheless, just as in the previous instance, in which the battery was supposed to consist of three elements, there will be a difference in the effect produced according to whether the external or internal resistance is neglected, since although the electro-motive force does remain unchanged, the increase in the size of the plates must be followed by a proportional diminution in their resistance which permits a proportional quantity of electricity to pass through them. Let us first suppose that the external resistance, or r, be so much smaller than the internal or R, that it can be neglected, and that the plates have been enlarged three n times, then we will obtain from equation $I = \frac{E}{R + r}$ (3) $I = \frac{nE}{R} = nI$ (8). That is to say, by enlarging the plates of the element n, or three times (Fig. 246), when the external resistance is small, the intensity is increased correspondingly. On the other hand, suppose the internal resistance, or R, is so small that it can be neglected, then equation $I = \frac{E}{R + r}$ (3) will become $I = \frac{E}{r}$ or $I = I$ (9). That is to say, by enlarging the plates of the element n, or three times, when the internal resistance is small the intensity is not increased. Resuming what has just been said, we learn by Ohm's law that if the internal resistance be small, it is of advantage to increase the number of cells; on the other hand, if the internal resistance be large, while it is of no advantage to increase the number of cells, it is of advantage to enlarge the plates of the cell, nothing, however, being gained by enlarging the plates if the internal resistance be small. It need hardly be added that while the intensity or quantity of electricity flowing through the circuit in a given time remains the same, the density of the current may, however, vary, the latter being inversely as the cross section of the conductor—that is, the less the cross section, the greater the intensity.

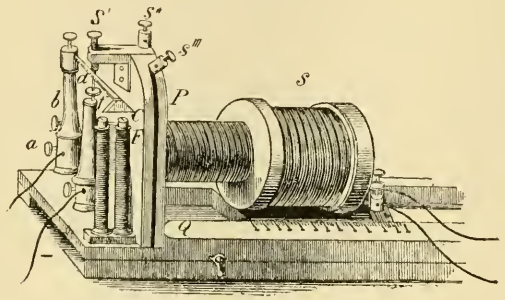
FIG. 246.

Galvanic element.

As, in the stimulation of the nerves by electricity derived from

the batteries just described, we ordinarily make use of the induction apparatus of Du Bois Reymond,[1] a brief description of that most useful instrument in this connection appears appropriate. As its name implies, it is an apparatus (Fig. 247) by means of which an induced current can be applied to a nerve, and in order that the

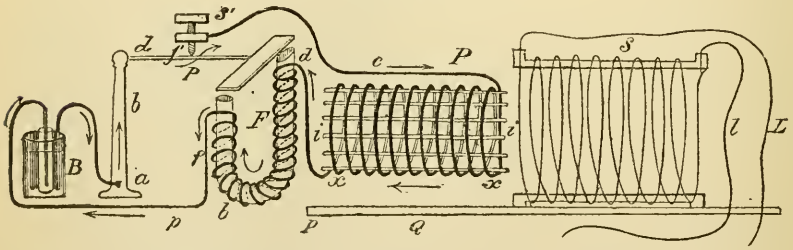
Fig. 247.



Du Bois Reymond's induction apparatus. (Landois.)

strength of the current may be varied at pleasure, the secondary coil S, to which the electrodes l L are attached, is placed upon a graduated slide (Q), so that it can be made to approach or recede from the primary coil P, as near or far as desired. The current

Fig. 248.



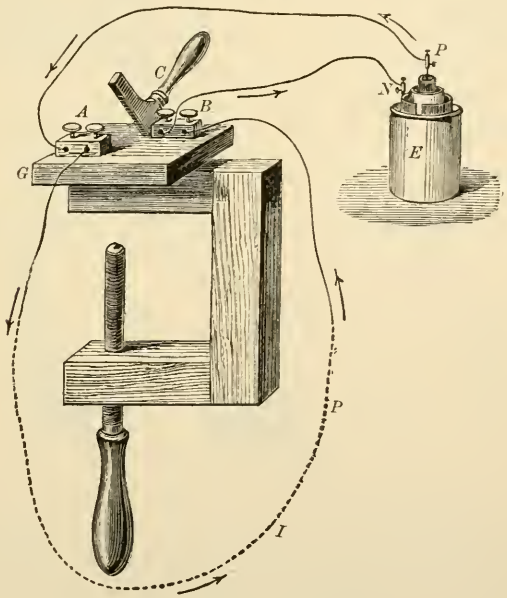
Schema of Du Bois Reymond's induction apparatus. (Landois.)

from the battery B (Figs. 247 and 248), entering the apparatus at the binding screw a, passes up the pillar b and through the German silver spring d, then through the primary coil P, and the coil F, returning to the battery by the binding screw p. As the current enters the primary coil P, an induced closing or making current is for the moment developed in the secondary coil S, and in an opposite direction to the primary current. During the passage of the current, however, through the coil F, the iron core within the latter becoming magnetized, the spring d is pulled down from the screw f, the result of which is that, the primary current being interrupted,

[1] Untersuchungen über thierische Electricität, Zweiter Band, s. 393. Berlin, 1849.

there is developed for a moment in the secondary coil *S* an induced breaking or opening current in the same direction as that of the primary current. As the iron cores within the coil *F* under these circumstances become demagnetized through the absence of the current, the spring *d* flies up again ; contact being again made with the screw *f*, the current passes, as before, through the primary coil, to be again broken with the magnetization of the core within the coil *F*, and to be again made with the demagnetization of the same, and so on indefinitely. The effect produced by the iron core within the primary spiral is the same as that of the primary spiral itself, since in being magnetized and demagnetized through induction by the making and breaking of the primary circuit, the core induces closing and opening currents in the secondary spiral similar to

FIG. 249.



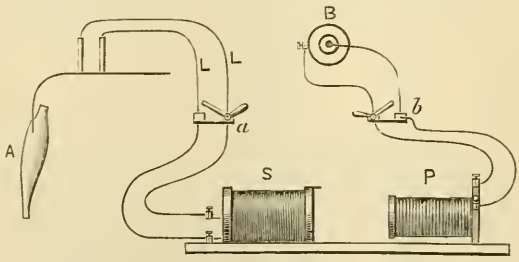
Du Bois Reymond's key.

those due to the making and breaking of the current in the primary one. By applying the electrodes *l L* attached to the secondary coil, to the nerve, the latter will be stimulated by the making and breaking induced currents, and which so rapidly succeed each other that the muscle is soon brought into a state of tetanus. If, however, it is desired to stimulate the nerve by a single induction shock —that is, by one closing and one opening induced current, then the wire of the battery must be attached to the binding screw *S'* instead of to *a* (Fig. 247), a Du Bois Reymond key (Fig. 249) having also been inserted within the circuit of the primary coil. The key being down, the current will then be short-circuited—that is, will pass

directly back to the battery *E*, since the resistance offered by the key is less than that offered by the nerve.

With the elevation of the key, however (Fig. 249), the current will pass through the primary coil p, developing the closing, or making induced current in the secondary coil S as before ; but, as the current through the primary coil is not broken through the fall of the spring, the wire being attached in this experiment to *S'* (Fig. 247), there will be no opening or breaking current induced in the secondary coil. The latter is, however, at once developed in the secondary coil by simply depressing the key, the current being then short-circuited again, it returns back to the battery without passing through the primary coil. It will be observed that when the induction apparatus is so arranged and used, that the nerve is stimulated once by the current induced by the closing of the primary circuit, and once by the opening of the same. Suppose, however, it be desired to stimulate the nerve by only the closing or the opening current? To accomplish this, a second Du Bois Reymond key (Fig. 250, *a*) must be also inserted within the circuit of the secondary coil S, and the two keys worked in the following manner: We will suppose, at the beginning of the experiment, that the key *b*, within the cir-

Fig. 250.

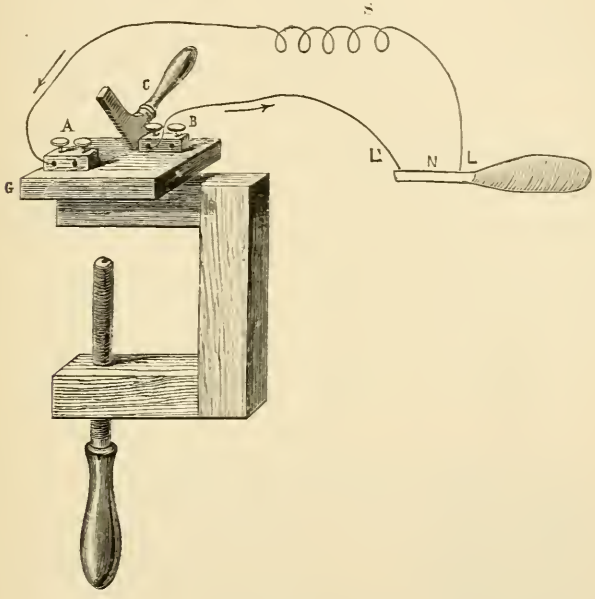


Stimulation of nerve by closing or opening current.

cuit of the primary coil P, is down, and the key *a*, within that of the secondary coil S, is up, then with the elevation of the key *b*, and the passage of the current from the battery through the primary coil, there will be developed for an instant in the secondary coil an induced current, and the nerve will be stimulated by a closing or making single induction shock. The key *a* should now be depressed so that the nerve will not be stimulated by the opening or breaking of the current in the primary coil, due to the depressing of the key *b*, and the consequent short-circuiting of the current. The nerve has then been stimulated by the closing of the current only. Supposing the two keys to be both down, let us now elevate the key *b* ; the secondary current developed in consequence will not influence the nerve as in the preceding experiment, since the key *a* being down, the secondary current is short-circuited. If, however, now the key *a* be elevated, and the key *b* depressed, the secondary

current developed through the breaking of the primary current will be transmitted to the nerve, and the latter will be stimulated by the opening or breaking current only. Whether it be desired to stimulate the nerve by a single induction shock, or many successive ones, or by the secondary current induced through the making or breaking of the primary one, the key should always be used as a short-circuiting one (Fig. 250) rather than as a simple friction key (Fig. 251), since in the latter case muscular contraction may be produced

FIG. 251.

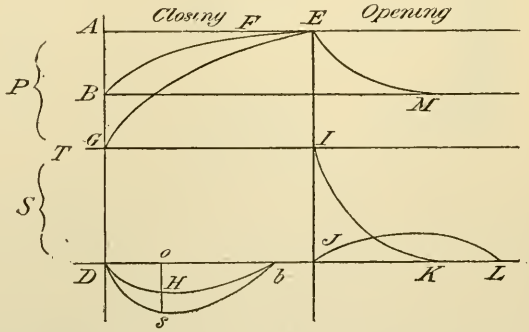


Simple friction key.

by unipolar induction. While no secondary current is induced in S (Fig. 251) by that in the primary, the secondary circuit being broken through the key being open, free static electricity may be given off at the end of the single electrode (L), and transmitted through the nerve to the muscle, the electricity previously accumulated at the end of the electrode being due to the decomposition of the neutral electricity in the secondary coil, induced by that in the primary coil, as takes place in the prime conductor in working the ordinary electrical machine. If, however, the secondary coil be short-circuited by a Du Bois Reymond key, as in Fig. 250, the key being down, then the secondary circuit being perfectly closed, a secondary current will be developed, and unipolar induction prevented, the current passing directly back through the coil, and none passing into the nerve, which, as we have just seen, is not the case, the key being used, as a friction key (Fig. 251), and open. When, however, the short-circuiting key is opened, and the secondary

circuit is completed by the nerve intervening between the electrodes, the circuit being but imperfectly closed, unipolar induction may occur even then, as when the key is used as in Fig. 251. If, however, there be any doubt as to whether the muscular contraction be due to the stimulus exerted by the nerve excited by the secondary current, or to the unipolar induction shock—that is, the direct transmission of the static electricity through the nerve to the muscle—it can be at once decided by simply dividing the nerve between the lower electrode and the muscle, since, if contraction then ensues, the ends of the nerves being approximated, it must be due to unipolar induction, and not to the nerve, as the division of the nerve does not interfere with the transmission of the electricity, but makes impossible that of the nerve force. It may be mentioned, in this connection, that the surest way to avoid unipolar induction is to put the upper electrode in communication with the earth through the gas or water pipe of the laboratory by a good conductor, and in so leading the free electricity off, prevent it influencing the muscle, and so effecting the contraction due to nerve excitement, as brought into activity by the secondary current alone. It will be seen, presently, that if a nerve be stimulated first by a closing, and then by an opening induced current, that the physiological effect due to the latter, as shown by the extent of the muscular contraction, is greater than that due to the

FIG. 252.[1]



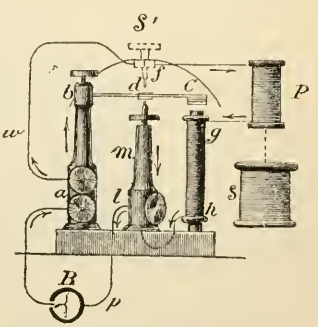
Graphic representation of effect of the extra currents on the induction currents.

former. Now, it is desirable, under certain circumstances, that the two currents should be equalized as far as possible. To appreciate the manner in which this is accomplished, it will be first necessary, however, to explain briefly why the induced opening current is more powerful than the closing one. Inasmuch, as with the closing of the current in the primary coil, there is developed, momentarily, a current in the secondary one, opposite in direction to that of the primary, it might be supposed that, in a similar manner, the indi-

[1] Du Bois Reymond, Gesammelte Abhandlungen, Erster Band, s. 236. Leipzig, 1875.

vidual coils of the primary current would act inductively on each other. Such is found to be experimentally the case, the current so produced, and opposite in direction to that of the inducing current, being known as the inverse extra current. The latter, being opposite in direction to that of the inducing current, must weaken it, and it is on account of this retarding influence of the inverse extra current that the closing primary current only gradually attains its maximum intensity, as may be represented graphically (Fig. 252) by the curve line *G E*, in which the horizontal line *T* represents the duration of the current. The corresponding closing current, induced in the secondary coil, may in the same manner be represented by the curve *D s b* only the ordinate *o s* must be drawn below the line *D J*, since the current is in the opposite direction to that inducing it. In a similar manner, at the moment of the opening of the primary current, there is developed within the primary coil a direct extra current, so called on account of it being in the same direction as the current inducing it, and therefore intensifying it. But, as there is no arrangement in the ordinary induction apparatus by which the primary current is maintained, the direct extra current is suppressed at the opening of the primary current, the latter is therefore suddenly interrupted when at its full strength, and may be represented graphically by the perpendicular line *E I*, and the opening current in the secondary coil by the perpendicular *J I*, it being in the same direction as that in the primary, and which, having attained its maximum suddenly, falls off more gradually, as shown by the curve line *I K*. From the sudden manner in which the opening current developed in the secondary coil attains its maximum intensity *J I*, as compared with the gradual increase of the closing one *D b*, it becomes evident why the effect of the stimulation by the former current is greater than that by the latter. Such being the case, the induction apparatus being used as just described, let us modify the instrument a little, as done by Helmholtz,[1] by connecting the binding screw *a* (Fig. 253), by means of a wire (*w*), with the binding screw *S'*, and lowering the silver spring (*d*) away from the point of the binding screw, the current will then pass by the connecting wire *w* directly into the primary coil *P* without passing first along the spring, and from the primary coil back to the battery by the coils *g h;* but with the magnetization of the core within the latter the spring will be lowered, and

Fig. 253.

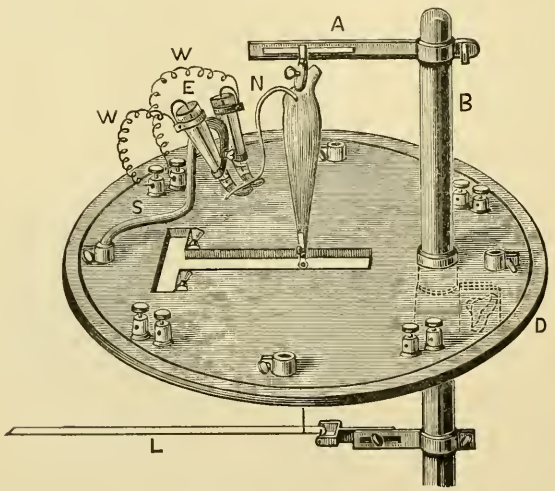


Helmholtz's modification of induction apparatus.

[1] Du Bois Reymond, op. cit., s. 231.

the greater part of the current being short-circuited will then pass directly back to the battery by the spring *d* and pillar *m;* the primary current being then weakened, as represented graphically to the extent of the lines *A B* (Fig. 252), the magnetization of the core within the coils *g h* (Fig. 253) will not be sufficient to keep the spring down, the short circuit current will be reopened, and all the current will pass through the primary coil again. The Helmholtz modification of the induction apparatus being used, as just described, it will be observed that, as the current in the primary coil is never entirely interrupted, the direct extra current developed at the moment of the opening of the primary current within the latter will reinforce the primary current, the two currents having the same direction. The partial interruption of the primary current, and the development of the opening secondary current will, therefore, be both gradual, as shown by the curves *E M* and *J L*, respectively, which is not the case, as we have seen,

FIG. 254.



The moist chamber, with the nerve-muscle preparation, non-polarizable electrodes, and lever in position ready for an observation. The glass cover is not shown.

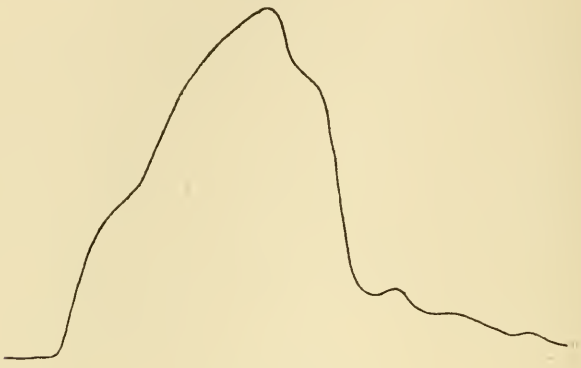
when the ordinary induction apparatus is used, since the primary current, being entirely interrupted, the direct extra current cannot make this reinforcing effect felt. The opening secondary current *J L*, with Helmholtz's modification, attaining then its maximum intensity, gradually, like that of the closing secondary one *D H b*, differs but little in its physiological effects from the latter when used as a stimulus.

That part of the sciatic nerve supplying the gastrocnemius muscle in the frog being the one that we shall make use of in our experiments, on account of its length and the readiness with which it

is exposed, it may be mentioned that in preparing the nerve it should be touched as little as possible, and never seized with a pair of forceps, though it must be completely separated from the adjacent nerves. The gastrocnemius muscle, the contraction of which we take as a measure of the stimulation of the nerve, having been cut through at its insertion the tendo Achillis, must be completely freed up to its origin at the end of the femur; of the latter enough should be left so that it can be firmly clamped to the bar A (Fig. 254), of the upright B, the tibia and fibula being, however, entirely removed. If the nerve-muscle preparation so prepared and clamped be covered with a glass bell fitting into the rim of the disk D, of ebony or other hard wood a few pieces of wet blotting paper, having been previously placed upon the disk, the nerve and muscle will be prevented from getting dry. The disk is also provided with binding screws for receiving the wires from the secondary coil of the induction apparatus, and from the electrodes E supporting the nerve N. The electrodes should be non-polarizable—that is, electrodes which, while transmitting the current from the secondary coil of the induction apparatus, will not generate a current by contact with the nerve. Of the different forms of non-polarizable electrodes a convenient one is that consisting of a glass tube (Fig. 254, E), bent and plugged up at one end by a putty made of china clay and 0.75 per cent. solution of sodium chloride, and containing a saturated solution of zinc sulphate, into which is immersed to a depth of about 3 mm. a slip of thoroughly amalgamated zinc. The wires W W leading to the binding screws are attached to the latter, which is usually sufficiently strong to hold up the electrodes; if not, the latter can be movably clamped to the upright B, or supported as in Fig. 254, by an electrode bearer S. The glass tube is often closed at its extreme point, the plug of clay being exposed only where the small orifice has been drilled. Through an opening in the disk of the moist chamber the muscle can be attached to a lever (Fig. 254, L), and its contractions made very evident by the elevation of the latter. If the point of the lever be terminated by a brush or pen, by means of the blackened cylinder already described, a graphic representation of the muscular contraction can be obtained and preserved for future reference. The lever consists of a thin slip of wood, the portion near the fulcrum being of metal and perforated or notched to receive the hook attached to the tendon of the muscle, and has usually suspended from it a scale pan containing counterpoising weights varying from between 10 to 200 grammes. The moist chamber being so attached to the recording apparatus by means of its upright, that the point of the lever is brought in contact with the blackened surface of the cylinder, the latter is made to rotate for a moment so as to obtain first a base line. The nerve is now stimulated by the induction apparatus, first by a closing and then by an opening shock, without Helmholtz's modification being used, and the cylinder being made to rotate rap-

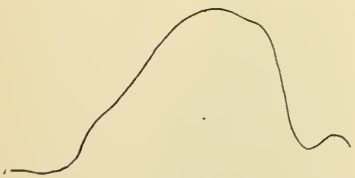
idly it will be observed that the lever is elevated higher in the latter case (Fig. 255) than in the former (Fig. 256), the effect of the opening shock being greater than that of the closing one for the reasons already given.

Fig. 255.



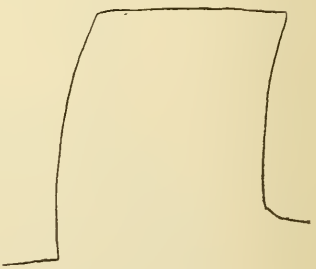
Opening shock.

Fig. 256.



Closing shock.

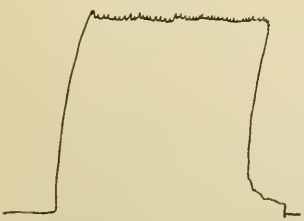
Fig. 257.



Curve of tetanus.

If, however, the nerve be stimulated by a series of closing and opening shocks the magnetic interruptor of the induction apparatus being used, the lever is observed to remain elevated (Fig. 257), the interval between each shock being of so short a duration that the lever descends but a little distance when it is elevated again. The elevations and depressions of the lever due to the individual contractions of the muscle when so rapidly produced, are, however, soon lost to view, becoming so fused together that they are not, therefore, apparent in the trace of the muscle curve of tetanus. The slight fall and rise of the lever become, however, quite evident if the primary current be interrupted, not by the magnetic arrangement (*d*, Fig. 248), but by a reed like that

Fig. 258.



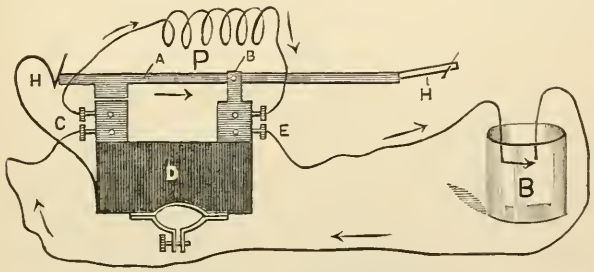
Muscle curve. Primary current interrupted sixteen times a second.

already described, vibrating at the rate of sixteen times a second, placed between the primary coil and a key, as shown by the trace (Fig. 258), obtained in this manner.

It will be observed that in the preceding experiments in which electricity was made use of as the stimulant to call into activity the nervous irritability, muscular activity being taken as the measure of the latter, that three distinct forms of energy are involved, electricity, nervous, and muscular. That the electricity acts simply as a stimulant is evident, since it is only transmitted across the nerve transversely from electrode to electrode, and that the nerve impulse is gradually transmitted from the point where the nerve is first excited by the electricity to the muscle, is proved, as will be shown presently, by the length of time that is required by the nerve force to traverse the nerve to the muscle, and from the death of the nerve progressing gradually from its cut end to the periphery. Further, just as electricity is to be distinguished from nerve force, so is the latter to be distinguished from muscular force. Indeed, the effect of nerve force can be prevented by curara, the latter substance probably acting by destroying the nerve endings, the muscular force, however, remaining unaffected, whereas the latter force is destroyed by sulphocyanide of potassium, the nerve force being unaffected.[1]

If in stimulating a nerve the electrodes be applied to the latter as near as possible to the muscle, a marking lever (Fig. 259) and

FIG. 259.



The marking lever.

chronographic apparatus being used at the same time, the moment at which the nerve is stimulated will be recorded upon the cylinder by the depression of the point of the lever, the current previously short-circuited through C A B E being then thrown into the primary circuit C H P E and inducing a current in the secondary one. The marking lever having been placed in contact with the cylinder above the pen of the chronograph and below that of the muscle lever (Fig. 260) it will be observed that usually 0.01 sec. to 0.004

[1] Bernard, Systeme Nerveux, T. i., p. 198. Paris, 1858. Vulpian, Physiologie et comparée du Systeme Nerveux, p. 186. Paris, 1866.

sec. elapses, as determined by the chronograph between the stimulation of the nerve and the contraction of the muscle, the short period of time so intervening being known as the "latent period." In order

FIG. 260.

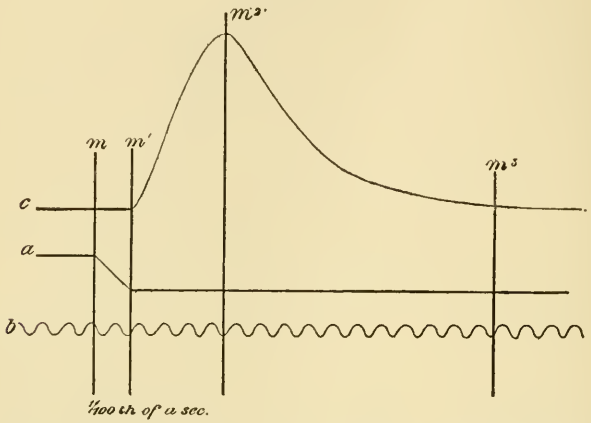
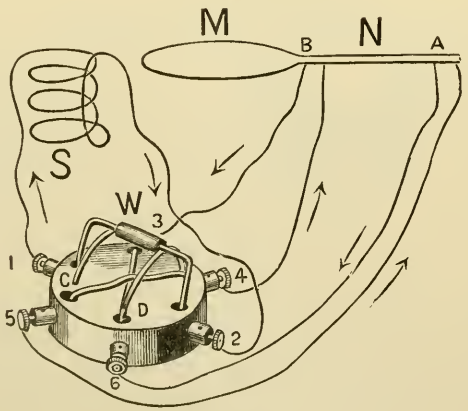


Diagram of a muscle curve as drawn on a traveling surface. *c*. The line described by the point of the lever connected with the muscle. *a*. The line described by marking lever. *b*. The line described by the tuning-fork. The vertical line *m* marks the moment of stimulation, m^1, the beginning; m^2, the maximum; and m^3, the end of the contraction of the muscle. (FOSTER.)

to avoid misunderstanding, it may be mentioned in this connection that a distinction is often made between the so-called electrical latent period and the mechanical one just referred to, the former lasting in

FIG. 261.



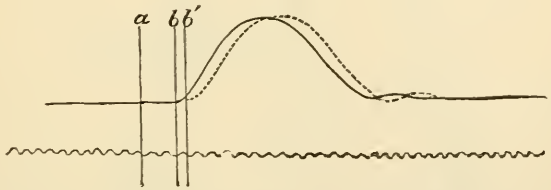
Whippe.

the striated muscles of the frog a shorter time (0.002 sec.) than the latter (0.004 sec.).[1] If the nerve be stimulated not where it passes

[1] W. Biedermann Electrophysiologie, 1895, s. 48. Burdon Sanderson, Centralblatt für Physiologie, 1890, —. Tigerstedt, Archiv für Anat. u. Phys., 1885, s. 111.

into the muscle, but at some distance from the latter, 2.5 cent. (1 inch), say, as at A (Fig. 261), which can be readily done by simply placing the wires C D of the whippe (the cross piece being left out) in the mercury cups in connection with the binding screws 5 and 6, it will be observed that not only 0.01 sec. (Fig. 262, *a b*) elapses between the stimulation of the nerve and the contraction of the muscle, but an additional very small period of time (0.0008 sec., *bb'*, Fig. 262) intervenes, which precedes that of the latent period. The difference in the interval of time elapsing between the stimulation and the contraction in the two cases is evidently due to the fact that in the case of the nerve being stimulated at A rather than at B, Fig. 261, the impulse must travel through a distance of 2.5 cent. (1 inch) before it reaches the muscle, and as in doing this 0.0008 sec. elapses, it may be inferred that nerve energy is propagated approximately at the rate of 28 meters (91.8 feet) per second.

FIG. 262.



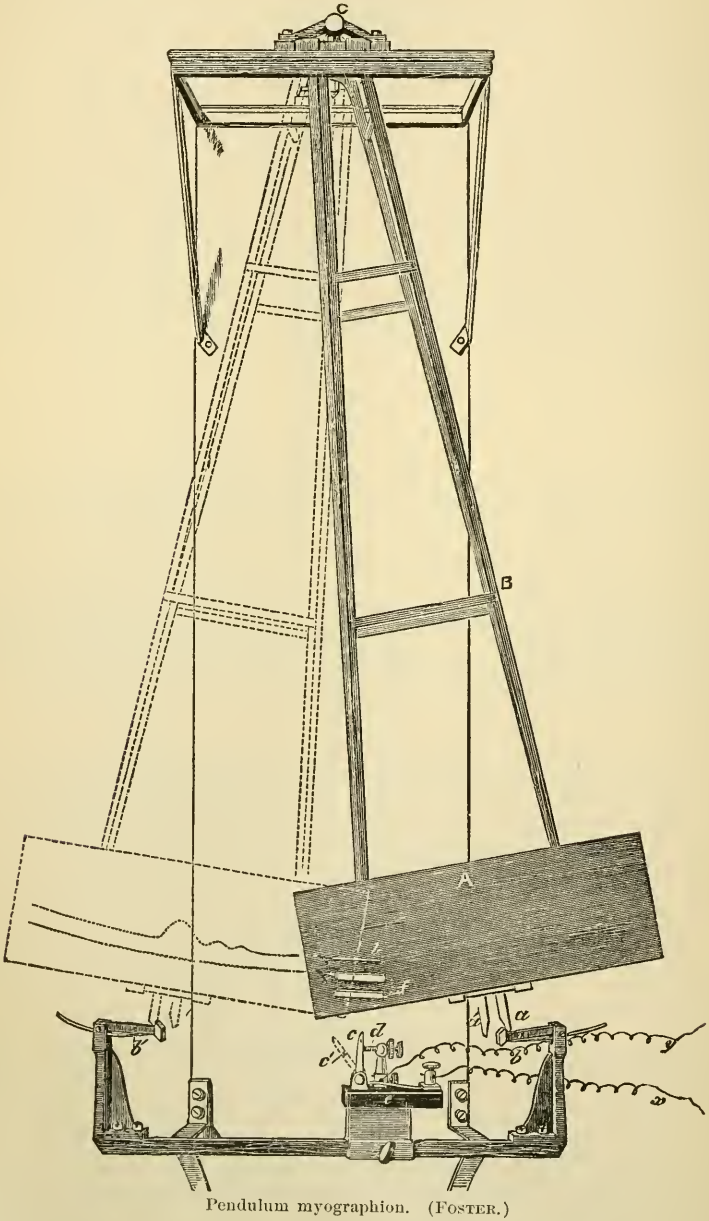
Curves illustrating the measurement of the velocity of a nervous impulse. (Diagrammatic.) To be read from left to right. *ab*. The interval of time elapsing between moment of stimulation and contraction of muscle when nerve stimulated at entrance of latter into muscle. *ab'*. The interval when nerve stimulated at some distance from muscle. *ab*. Latent period in both cases. *bb'*. Interval of time during which nervous impulse travels along nerve to muscle. It is to be understood that the interval of time *bb'* precedes that of *ab*, the nerve being stimulated at *a*. (FOSTER.)

The nerve force is probably, however, transmitted at a slower rate in the nerves of the frog than that just given, since, if a long nerve be stimulated in three different places, near the muscle, midway, and above, the curves show that more than double the time elapses during the passage of the nerve force through the whole nerve than from the middle point to where the nerve passes into muscle.[1] While the latent period and the velocity with which nerve force is transmitted, can be determined in the manner just described, a more accurate method is by means of the pendulum myograph.

The pendulum myograph (Fig. 263) consists, as its name implies, of a pendulum suspended by a knife edge, working upon a support firmly fixed by a frame imbedded in the wall of the laboratory. The pendulum carries two glass plates, the outer smoked one, A, serving as a recording surface, the inner one, not seen in the figure, as a counterpoise. The plate A, as the pendulum vibrates, pushes aside by its tooth *a'* the bar *c*, thereby interrupting the primary current *xcdy* of the induction apparatus, and also a current passing through the small electro-magnet, to which is attached a pen serv-

ing as a marking lever. The pendulum, having reached b', is held there by a catch similar to that which held it at a before its vibration began.

Fig. 263.

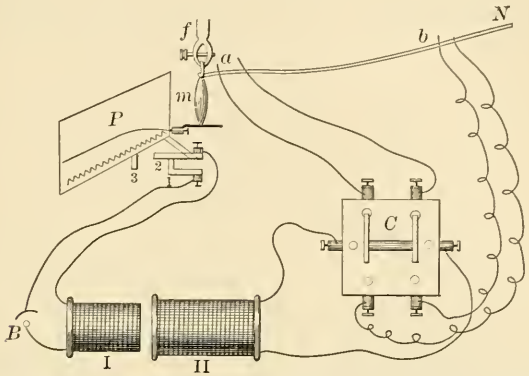


Pendulum myographion. (Foster.)

With the interruption of the primary current I (Fig. 264), the nerve is stimulated by the opening shock of the secondary current

II, transmitted to the electrodes, the moment of stimulation being determined by the moving of the pen acting as a marking lever, due to the simultaneous interrupting of the current passing through the small electro-magnet. The time elapsing is determined, as in the preceding experiment, by the electro-magnetic chronograph *f*. In using the pendulum myograph the muscle *m* is attached, as in

FIG. 264.



Schema for measuring the velocity of the nerve impulse with pendulum myograph. *f*. Clamp for femur. *m*. Muscle. *N*. Nerve; *a*, near, *b*, removed from *C*, whippe. II. Secondary; I, primary spiral of induction apparatus. *B*. Battery. 1, 2. Key. 3. Tooth on the smoked plate. (LANDOIS.)

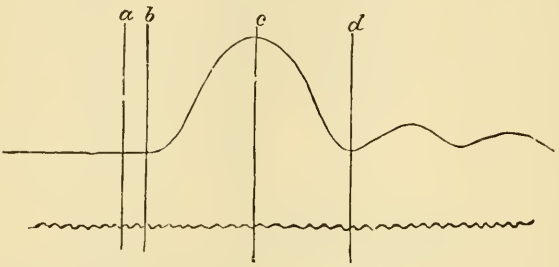
the preceding experiment, to a lever; the latter is, however, in this case much heavier, and is provided with a projecting steel point, which, in being pressed against the smoked plate *P*, makes the curved line, as the plate is carried past by the vibration of the pendulum. To demonstrate the rapidity with which the nerve force is transmitted, we make use of the whippe, as in the preceding experiment, throwing the current, by means of the latter, into the nerve at *b*, a definite distance from the point first stimulated *a*. The result, as shown by a tracing (Fig. 265) taken with the pendulum myograph, is the same as when obtained by the cylinder. In order to preserve the tracing on the smoked glass the latter is placed upon sensitive paper and exposed to sunlight.

The rate at which nerve force is transmitted has been determined by Helmholtz and Baxt,[1] in man as well as in the lower animals. In the case of the motor nerves this was accomplished by applying electrodes to the skin over the median nerve at the wrist, elbow, and upper arm, the arm being firmly surrounded by gypsum, except at the points stimulated. The time elapsing between the application of the electrodes and the muscular contraction, the latter being evinced by the swelling of the muscles of the ball of the thumb against a delicate lever, was greater when the stimulus was applied to the upper arm than at the wrist. The average rate of transmission was determined to be about 33.9 meters (111 feet) per second, varying, how-

[1] Monatsber. d. Berliner Acad., 1867, s. 228; 1870, s. 184.

ever, according to the temperature; being more rapid at a high than at a low one. The rate of transmission of the nerve force in sensory nerves was also determined by Helmholtz[1] in essentially a similar manner. A tactile impression being made successively upon the foot, thigh, and loins, the moment at which the sensation is felt is indicated in each instant by a movement of the finger. Now, since the time elapsing during which the impression becomes conscious perception in the brain, as well as that during which the nerve force is transmitted by the motor nerve to the finger, is the

FIG. 265.



$\frac{1}{100}$, $\frac{1}{20}$, $\frac{1}{25}$, of a second.

A muscle-curve obtained by means of the pendulum myograph, the nerve being stimulated at *a* (Fig. 264). To be read from left to right. *a* indicates the moment at which the induction-shock is sent into the nerve, *b* the commencement, *c* the maximum, and *d* the close of the contraction. The two smaller curves succeeding the larger one are due to oscillations of the lever. Below the muscle-curve is the curve drawn by a tuning-fork making 180 double vibrations a second, each complete curve representing therefore $\frac{1}{180}$th of a second. It will be observed that the plate of the myograph was travelling more rapidly toward the close than at the beginning of the contraction, as shown by the greater length of the vibration curves. (FOSTER.)

same in all three cases, the differences observed in the successive observations must be due to the different lengths of the sensory nerves transmitting the impression, the average rate, according to Helmholtz, being about 60 meters (196 feet) per second, modified by the temperature, as in the case of motor nerves.

It would appear, however, from recent researches[2] that the rate of conduction of nervous impulses is about the same in sensory as in motor nerves, viz., 35 meters (115 feet) per second.

Knowing the rapidity with which nerve force is transmitted through the peripheral nerves, its rate of transmission through the spinal cord in man can be inferred from the difference in time elapsing during the passage of a voluntary impulse from the brain through the cord to the upper and to the lower extremity, or in the reverse direction, of an impression made upon the periphery, giving rise in the brain to a sensation. Thus, in the case of the motor fibers of the cord, if the hand be moved first in obedience to the will, and then the foot, it is evident that a longer period will elapse between the application of the stimulus, the will, and the muscular contraction, in the latter case than in the former, since,

[1] Physo-Ocon Ges. zu Königsberg, 1850, Dec. 13.
[2] Oehl, Archiv italiennes de Biologie, xxi., 3, 1895, p. 401.

in the transmission of the nerve force through the spinal cord to the sciatic nerve, three times the distance has been traversed as in its transmission to the median nerve. In this way it has been shown by Burckhardt[1] that the average rate of transmission of the nerve force through the motor fibers of the cord, is about 10 meters (33 feet) per second, or about one-third of that of the motor fibers of the peripheral nerves. On the supposition that 0.08 sec. elapses during the passage of the nerve force from the brain to the foot, one-half of that time is consumed in its transmission through the cord, and one-half through the nerves. The rate of transmission through the sensory fibers of the cord does not differ very much, however, from that of the sensory fibers of the peripheral nerves. Supposing that the distance traversed through the sciatic nerve and cord from the periphery to the sensorium by a sensory impulse be the same as that of the motor impulse just referred to, the time elapsing between the application of the stimulus and the resulting sensation would be about 0.025 sec.

As an illustration of the relative slowness with which nerve force is transmitted, it may be mentioned that a whale one hundred feet long would not feel the wound of a harpoon until one second after the weapon was thrust into its tail, and that in response to a voluntary impulse, about one second would elapse before the tail would be moved, supposing that the nerve force is transmitted in the huge cetacean at the same rate as in man. It should be mentioned, however, in this connection according to Burckhardt, that tactile impressions appear to be transmitted much more rapidly through the spinal cord than painful ones, the former at the rate of 42 meters (137 feet), the latter 13 meters (42 feet) per second. The latent period and the velocity with which the nerve force is transmitted through the spinal cord being known, it becomes possible to determine approximately at least the time required for the apprehension or perception by the brain of an impression and volition. Thus, supposing the interval of time elapsing between the production of a sound and the hearing of the same has been determined to amount to 0.198 sec., it follows that if we deduct from the latter the time during which the nervous impulse is transmitted through the acoustic nerves, spinal cord, motor nerves and latent period, 0.086 sec., the remainder, 0.112 sec., will be the time required by the brain for perception and volition.

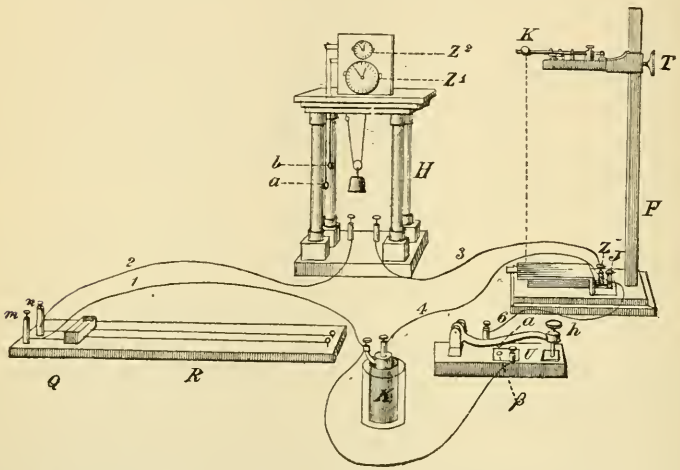
Transmission through acoustic nerve . .	0.010 sec.
Perception and volition	0.112 "
Transmission through spinal cord . . .	0.022 "
" " motor nerve . .	0.044 "
Latent period	0.010 "
	0.198 "

The interval of time (0.198 sec.) elapsing between the production of a sound and the hearing of the same may be determined among

[1] Die Physiologische Diagnostik, s. 32, Leipzig, 1875.

other methods by means of the apparatus (Fig. 266) in which the clock-work of the Hipp's chronoscope *H*, held by an electro-magnetic anchor is set going through the weaking of the current *K1mn2H3Z4* when the latter is short-circuited through *K3a6JZ4* by the tilting up of the board through the electrodes *JZ* by the falling of the ball, the cause of the sound and which is stopped by the voluntary elevation of the lever *h* at the instant that the sound is heard.

FIG. 266.



Apparatus for determining the interval elapsing between the production and hearing of a sound. (WUNDT.)

The determination of the interval between the production of a light and the seeing of the same can be determined in a similar manner by suitable apparatus. Such determinations, apart from their physiological interest, are also of practical importance to astronomers, it being well known to the latter that considerable difference exists, amounting in some instances to as much as one second, between observation made upon the transit of a star for example, the object being seen by one observer sooner than the other. Indeed, it was such discrepancies that led Hirsch [1] to determine, as far as possible, the "reaction time," that is the interval which elapses between the application of the stimulus and the making of the signal when the sensation is felt, of the rapidity with which impressions are transmitted through the optic and acoustic nerves and perceived by the brain, and of so ascertaining the personal error due to individual peculiarities, and by means of which the observation could be corrected by the personal equation, as it is called.

The determination of the rapidity with which nerve force is transmitted is a striking illustration of the advances made in phys-

[1] Bull. de la Soc. des Sciences nat. de Neufchatel, 1862.

iology, due to the introduction in its study of physical methods. In the year 1844 Johannes Muller expressed the view that "we shall never have the means to determine the rapidity of nerve action, as the comparison of immense distances is wanting, by which the rapidity in the nerves can be calculated in the same respect as in the case of light,"[1] and yet within six years of this period what was considered impossible by one of the greatest biologists was actually accomplished, as we have seen, by Helmholtz.[2]

[1] Physiologie, i., 4 Aufl., s. 581. Coblenz, 1844.
[2] Monatsber. d. Berliner Acad., 1850, s. 14.

CHAPTER XXVIII.

THE NERVOUS SYSTEM.—(*Continued.*)

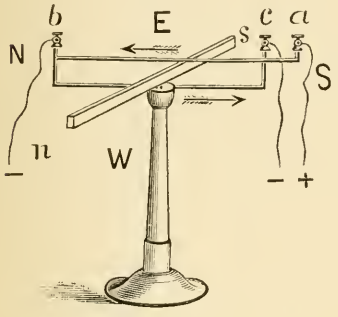
GALVANOMETERS. NON-POLARIZABLE ELECTRODES. ELECTRICAL CURRENT. ELECTRO-MOTIVE FORCE AND RESISTANCE OF NERVES. CAUSE OF ELECTRICAL CURRENT OF NERVES.

It will be observed, in the preceding experiments, performed with the view of demonstrating nervous irritability, that the muscular contraction following the stimulation of the nerve is the only visible positive evidence that we have obtained so far of the nerve having been modified in any way by the application of the stimulus. That some change, however, must be set up at the point of irritation and transmitted thence through the nerve is evident from the fact of the muscle contracting in response to the stimulus, though the latter be applied to the nerve at a distance from the muscle, while from the slowness with which the irritation is transmitted thence through the nerve, it is to be also inferred that the change in its condition during a state of activity, whatever the nature of the change may be, is of a gradual character. If, however, the electrical condition of the nerve be examined in a state of rest, and in one of activity, it will be learned that the change induced in a nerve through its stimulation, is a change partly at least in its electrical condition, since the natural electrical current that is present in a cut nerve during a state of rest, disappears during one of activity. Indeed, it can be shown that as rapidly as the electrical current disappears in the nerve, the nerve current or irritability of the nerve appears, and it may be incidentally mentioned here, as confirmatory of what has just been said with reference to the disappearance of the electrical and the appearance of the nerve impulse, that the fact of the velocity of electricity and of the nervous impulse being at the rate of 288,000 miles a second and of 100 feet a second respectively, also proves the non-identity of the two. To appreciate, however, the change in the electrical condition of a nerve brought about during its state of excitement through the effect of a stimulus, it will be first necessary to explain the construction of the galvanometer, by means of which the presence of an electrical current in a cut nerve during a state of rest, and in an uninjured one of activity, cannot only be demonstrated, but also the amount and direction of the same determined.

The construction of a galvanometer is based upon the fundamental fact discovered by Oersted, in 1819, of a magnetic needle being

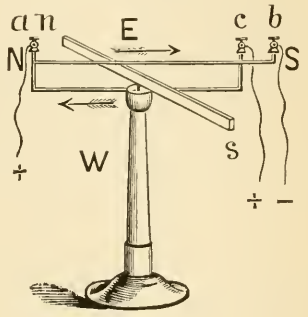
deflected out of the magnetic meridian by a current of electricity passed along a wire parallel to it. Thus, for example, if an electrical current be passed above the magnetic needle from south to north as indicated by the direction of the arrows (Fig. 267, *a b*), the north pole n of the needle will be deflected toward the west, while if in the reverse direction, from north to south (Fig. 268, *a b*), the north pole n of the needle will be deflected toward the east.

Fig. 267.



Deflection of magnet by currents.

Fig. 268.



Deflection of magnet by currents.

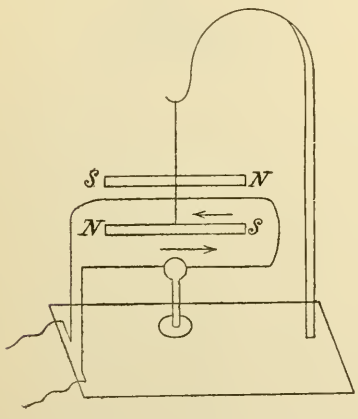
On the other hand, if the current be transmitted from north to south but below the needle, then the north pole of the needle will be deflected toward the west, as in Fig. 267, but if in the reverse direction toward the east, as in Fig. 268. The direction according to which the needle is deflected in either of the above cases may be easily remembered by the memoria technica of Ampère, according to which the north pole of the needle is always deflected toward the left of an individual supposed to be swimming in the electrical stream, and always facing the needle, the current entering the feet and leaving the head of the individual so disposed. That is to say, the north pole of the needle is always deflected toward the left of the current. It is evident, therefore, if a current be transmitted through a wire passed around a needle so that the current enters the wire at *a* and leaves it at *b* (Fig. 267), that not only will the north pole of the needle be deflected toward the west as the current passes above the needle from south to north, but still also to the west, as the current is transmitted below the needle from north to south, and that if the wire be coiled again and again around the needle and properly insulated, the deflection of the needle will be proportionally intensified. It need hardly be added that if the current be transmitted in the reverse direction, entering the wire at *c* and leaving it at *b* (Fig. 268), the needle will be deflected to the east. Hence, the name of multiplier given to such an instrument (Fig. 269), as invented in 1829, by Schweigger.

Fig. 269.

Multiplier.

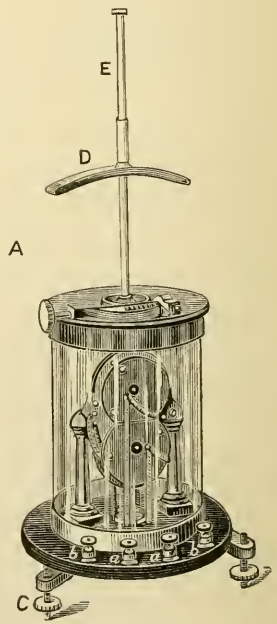
The magnetic needle is kept in the magnetic meridian by the magnetic current of the earth, the latter, in circulating around the globe from east to west, bringing parallel to itself and in the same direction the magnetic currents of the under surface of the needle, the latter finally coming to rest with the currents of its north pole, opposite in direction to that of the hands of a watch, and those of its south pole in the same direction, the needle, therefore, pointing north and south, with its currents at right angles to its long axis. It is obviously of advantage, therefore, in the construction of a galvanometer that the directive influence of the earth's currents, exercised upon those of the needle be eliminated, as the deflection of the needle by the directive influence of an electrical current passed through the surrounding wire will be then still more intensified. This was accomplished by Nobile, in 1827, by rendering the needle, or, rather, the needles, astatic, as it is called—that is to say, two needles (Fig. 270) *N S* and *S N*, are connected together, and

Fig. 270.



Astatic needles.

Fig. 271.



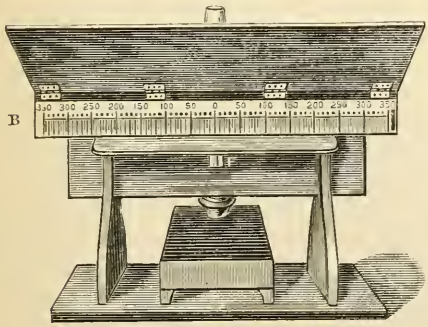
Thomson's galvanometer.

suspended by a fine silk filament, the lower one within the electrical circuit, the upper one above it, so that the north pole *N* of the lower needle is opposite the south pole *S* of the upper one, and the south pole *S* of the lower needle is opposite the north pole *N* of the upper one. Such being the disposition of the needles, the influence of the earth's magnetism exerted upon the north pole (*N*) of the lower needle is more or less neutralized through the same being exerted upon the south pole (*S*) of the upper one. In sensitive galvanometers this latter effect is still more thoroughly accomplished by placing a magnet D (Fig. 271), above the upper needle.

It hardly need be mentioned that, according to the Ampèrian

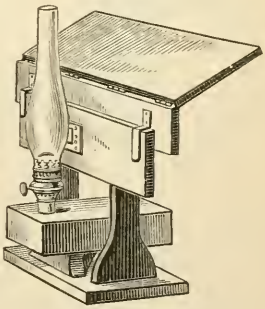
rule, the north end N of the lower needle, and the south end S of the upper one will move together, and toward the west, if the electrified current directing them be transmitted in the direction indicated by the direction of the arrows, for, though the upper needle $S\,N$ is subjected to the action of the two contrary currents below it, the action of the upper current being the nearest will influence it to the greatest extent. Upon the principles just enunciated are constructed the Thomson and Wiedemann galvanometers, both of which the author makes use of in determining the presence, intensity, and direction of the electrical currents of nerves. In Thomson's galvanometer (Fig. 271), the magnetic needles are very small and light, but highly magnetized, and are disposed in an upper and lower set, connected by an aluminium rod, and arranged astatically. Each needle is separately surrounded by numerous coils of very fine wire, ending in the binding screws, the course of the lower coil being opposite in direction to that of the upper one. To the upper set of needles is fixed a slightly concave mirror about 6 mm., or one-fourth of an inch in diameter, serving to reflect the beam of light back to the scale B (Fig. 272), the light being transmitted from the lamp through the narrow slit F under the scale, and the

FIG. 272.



Scale and lamp.

FIG. 273.



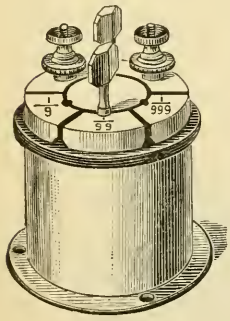
Lamp and scale for Thomson's galvanometer.

lamp placed back of the scale (Fig. 273). The astatic system of needles is suspended by a single fiber of silk from a brass pin fixed to the top of the vulcanite frame of the coils. The latter are supported upon brass uprights, and are covered by a glass shade fitting into the rim of a vulcanite disk, brass bound, which is levelled by three screws (CC). The brass-bound glass shade covering the uprights, supports a brass rod E, upon which slides a curved and weak magnet (D), serving to neutralize the earth's magnetism. When used, the galvanometer should be so placed that its mirror faces west, the light and scale being opposite the latter, and between two and three feet distant. The electrodes being attached to the outer two ($b\,b$) of the four binding screws, and the two intermedi-

ate ones (*a a*) being connected together, the current to be investigated will pass through the coils, the light moving from the zero along the scale to the left or right, according to the direction of the current.

If it be desired to compare the intensities of two electrical currents, then the connection between the two intermediate binding screws *a a* being unmade, the two electrodes conveying one of the currents must be attached to one of the outer binding screws (*b*), and the adjacent inner one (*a*), the other two electrodes similarly to the other outer binding screw (*b*) and the adjacent inner one (*a*). If the currents be equal in intensity, and opposite in direction, the mirror will be unaffected, and the light will remain at zero, only moving to the right or left, according as one or the other of the currents preponderates. It scarcely need be added that if a Thomson galvanometer be used in determining the presence, etc., of nerve currents, the room must be darkened. Inasmuch as this galvanometer is an exceedingly sensitive instrument, it is often desirable to allow only a fractional part of the current of electricity studied to pass into it, the remaining part of the current being shunted off. In accomplishing this object we make use of the electrical shunt. This instrument (Fig. 274) consists of a series of brass plates, separated from one another, but connected by wires of different lengths, which offer, therefore, more or less resistance to a current traversing them. The plates are, however, also capable of being more directly connected by means of a brass plug. The shunt is provided with two binding screws, to which are attached the two wires from the outer binding screws of the galvanometer and the two electrodes conveying the current, a part of which is to be diverted from the galvanometer.

Fig. 274.



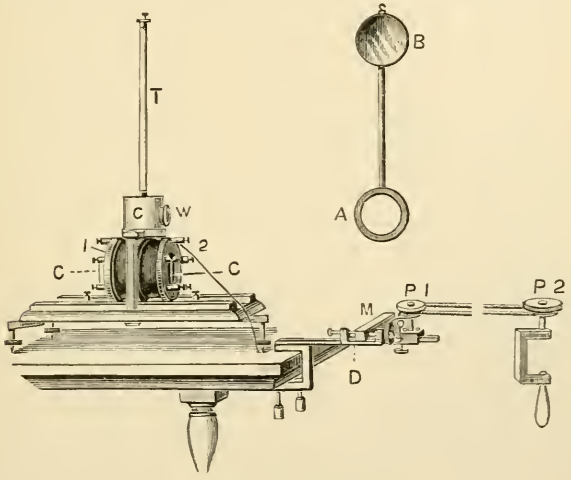
Shunt.

The two binding screws of the shunt can be brought into direct connection by turning down a brass bar; if this be done, the current from the nerve, for example, will be short-circuited, it passing from one binding screw to the other, back to where it came from, none of the current going to the galvanometer, owing to the resistance offered. If, however, the connection between the binding screws be unmade through the raising of the bar, and the plug not placed in any of the holes of the shunt, then the current, not being able to pass directly across from one binding screw to the other, will traverse the galvanometer. The coils of the shunt being graduated, however, according to the resistance of the galvanometer, by means of the plug, we can vary at will the proportional amount of the current going to the galvanometer to that short-circuited, the amount depending upon the ratio of the resistance of the gal-

vanometer to that of the shunt. Thus, for example, suppose the plug be inserted into the hole marked $\frac{1}{9}$, then such resistance is offered in the short circuit that only $\frac{1}{10}$ of the total current goes to the galvanometer, the remaining $\frac{9}{10}$ being short-circuited; if in the hole marked $\frac{1}{99}$, or $\frac{1}{999}$, then only $\frac{1}{100}$ or $\frac{1}{1000}$, respectively, of the current traverses the galvanometer, the remaining $\frac{99}{100}$, or $\frac{999}{1000}$, being short-circuited.

Weidemann's galvanometer, consists of a thick cylinder of copper (Fig. 275), through which a tunnel is bored, the latter capable of being closed at each end by either a cover with glass front, or by a solid plug of copper. Within the copper tunnel hangs a magnetized ring (Fig. 275, A), of such size that it can just swing clear

FIG. 275.



Wiedemann's galvanometer.

of the sides. The object in making the magnet ring-shaped is to make it stronger in proportion to its size, the center, or inactive portion of the magnet, in that form being absent. Connected with, and passing upward from the magnetized ring through a copper tube, is an aluminium rod, terminating in a light frame holding a circular plane mirror, facing east and west (B). In order to prevent currents of air moving the mirror, the latter is inclosed within a circular brass cover (C) having a circular window (W), through which the mirror can be viewed. Above the mirror is screwed a long glass tube (T), at the top of which there is a little windlass, supported by a small piece of ebonite, whose centering on the glass tube is effected by three screws. On the windlass a single fiber of silk is wound, passing through the ebonite and down through the glass tube, by means of which the magnet and mirror are suspended, the frame of the latter being pierced with an eye for the attachment of

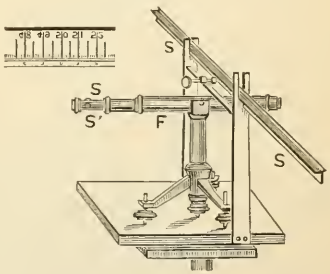
the platinum hook, to which the end of the silk fiber is looped. The magnetized ring can, by this means, be raised or lowered or centered in the copper chamber, the latter and its attachments being supported by brass columns on a mahogany plate, levelled by three screws. The coils C C, the turns of which in sensitive instruments, as in that of the author, may amount to as many as 30,000, and through which is transmitted the electricity exerting a directive influence upon the magnetized ring, are placed upon a sledge, that they can be so approximated as to meet right over the copper chamber, and when so disposed completely conceal the latter, as in Fig. 275. Since with the movement of the magnetized ring induced currents are set up in the surrounding copper chamber, opposite in direction to those of the needle, the oscillations of the latter are so diminished that after deflection it comes quickly to rest. The copper chamber is, therefore, called the damper, the close fitting of the ring within the latter and the proximity of the coils materially assisting in the dampening by it of the oscillations of the ring. Further, in order to render the magnetized ring within the copper damper astatic, we make use[1] of an accessory magnet (M), a Hauy bar, placed in the magnetic meridian horizontal to the needle, with its north pole pointing north, like that of the magnetized ring, and supported upon a bar (D) directed perpendicularly to the coils, and in a line with their axis. The accessory magnet can slide up and down the bar within its support, the bar being divided into centimeters, for measuring the extent of the movement. One end of the magnet being caught between a spring and a screw, and the latter being turned by the pulley P^1, the magnet can be moved from its spring end on the other end, forming an angle with the plane of the coils, the angular movement being effected by an experimenter seated at a distance by means of the pulley P^2. The galvanometer, being properly located, the accessory magnet, just described, is fixed upon its bar (B) by a clamp to the shelf. The magnet, being first placed at the end of the bar, is then slowly moved down it, the effect being gradually to neutralize the magnetic action of the earth. The moment, however, that the position of neutralization is passed the magnetic ring swings round, carrying the mirror, of course, with it, now facing north and south, so that its opposite poles are placed against the poles of the magnet, the movement involving a full half twist on its fiber. To prevent this, one of the copper plugs should be put in one of the openings of the chamber, by which the movement of the magnetic ring is blocked, the other opening being filled with a glass plug, the movement of the ring can be seen. This twisting tendency being observed, the accessory magnet should be moved back again till the tendency disappears, and the magnetic ring is just sufficiently influenced by the directive action of the earth to be kept in the meridian. The instrument will then be found to be very sensitive. When both coils are to be used, they must be connected by carry-

[1] Du Bois Reymond, Abhandlungen, s. 370.

ing a wire from a binding screw of the one to a binding screw of the other, according to the coils used, the remaining free binding screws receiving the wires conveying the current. When both coils enclose the copper chamber the most intense effect is obtained, the recession of coils from the chamber diminishing it.

The great advantage of Wiedemann's galvanometer is that by the copper damper the disposition of the coils C, and the accessory magnet M, the magnetized ring is made aperiodic or dead beat—that is to say, the magnetic ring, when affected by the current, swings around comparatively slowly, until the maximum deflection is reached, and arriving at this point it rests there without oscillation; the current being withdrawn, it swings back again to zero, stopping there without further oscillation, a current in the opposite direction being indicated, should it pass the zero. It is highly important in locating the galvanometer that no iron structures whatever should be present in its neighborhood. The instrument may be placed upon a strong wooden shelf fixed to a solid dry wall, or, if the laboratory or lecture-room be upon the ground floor, upon a pillar of concrete, capped with oak, built upon a solid stone foundation. In using Wiedemann's galvanometer in the laboratory the extent of the deflection of the magnetized ring is observed by means of an astronomical telescope, and of a scale (Fig. 276), supported by upright above and at right angles to the long axis of an astronomical telescope, the scale and telescope being placed upon the same table to which the pulley P^1, already referred to, is attached, and which ought to be from 6 to 9 feet distant from the galvanometer. The scale being directly opposite the mirror, the reversed numbers of the former will be seen in the latter in their natural position, and with the deflection of the needle the numbers will appear as if drawn across the mirror, the amount of the deflection being indicated by the number seen in the mirror when the needle comes to rest. For lecture purposes, however, the telescope, etc., is not used, a beam from a lime or electric light being received upon a small plane mirror, is thence reflected to the mirror of the galvanometer, and from the latter to a white scale placed at a distance of from 6 to 15 feet, according to the magnification desired. In this way the deflection of the magnetic ring can be made evident to a large audience.

FIG. 276.

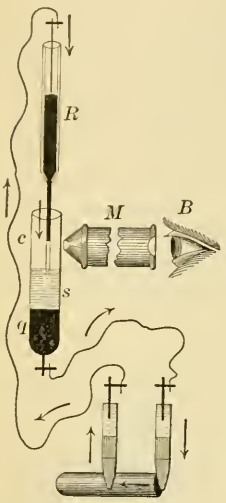


Telescope and scale.

A very sensitive instrument often made use of in determining the presence of electrical currents in nerves is the capillary electrometer of Lippmann. This consists (Fig. 277) of a capillary glass tube (*R*) filled from above with mercury and from below with

dilute sulphuric acid, and which opens by its lower narrow end into a wide glass tube (c) containing mercury (q) and sulphuric acid (s) and conducting wires terminating in non-polarizable electrodes. With the application of the latter to the nerve any electrical current present will be at once revealed by the movement of the thread of mercury in the direction of the arrow, as observed by the microscope, as a very slight difference of electrical potential causes a change in the surface tension of the mercury sulphuric acid meniscus.

FIG. 277.



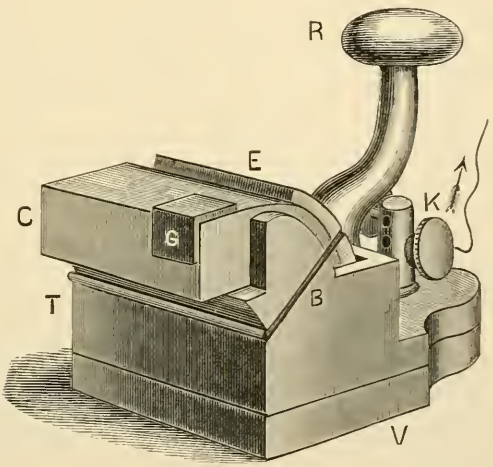
Capillary electrometer. *R.* Mercury in tube; capillary tube. *s.* Sulphuric acid. *q.* Mercury. *B.* Observer. *M.* Microscope. (LANDOIS.)

Inasmuch as in demonstrating the presence of an electrical current in a nerve by means of galvanometer, the current is conveyed by the wires passing from the binding screw to the nerve, it is obvious that these wires must terminate in non-polarizable electrodes—that is to say, as has been incidentally mentioned, in electrodes that will convey an electrical current already existing in the nerve examined, but will not generate a new one when placed in contact with the latter, since the latter current so generated, extremely weak though it may be in deflecting at once the needle, the galvanometer being so sensitive, might readily be mistaken for the pre-existing current whose presence we wish to demonstrate.

In order, however, to understand the manner in which the generation of the current is prevented by the contact of the electrodes with the nerve tissue, it will be first necessary to explain what is meant by the polarization of the electrodes, to which the above effect is due. Let us suppose that two platinum electrodes have been immersed in acidulated water, and that the electricity transmitted from the battery has decomposed the water, the positive pole being covered with bubbles of oxygen, and the negative with bubbles of hydrogen. If suddenly, now, the electrodes be disconnected with the battery, and connected with a galvanometer, the direction in which the needle of the latter is deflected will indicate the presence of a current, opposite in direction to that of the battery and weakening the latter, developed through the fact of the negative pole covered with hydrogen becoming positive to the positive pole covered with oxygen, just as in the case of non-constant batteries already referred to. It is the change in the condition of the electrodes which is known as their polarization, and which occurs in a similar manner if a nerve be placed upon two copper wires. We shall see hereafter that when a fresh muscle is connected with the galvanometer by copper wires, the deflection of the needle ensuing indicates the presence of a current, but which, on account of the polarization of the electrodes, may be as much due

to the generation of a current as to the presence of a preëxisting one. Even perfectly clean platinum electrodes soon become differently affected by contact with organic tissues, and so give rise to difference in electrical tension or electro-motive force. Regnauld, however, showed in 1854, that a strip of chemically pure zinc immersed in a solution of neutral zinc sulphate, and Matteuci, two years later, that ordinary zinc amalgamated and immersed in a saturated solution of the same, exhibited no polarization. Du Bois Reymond, availing himself of these discoveries, devised non-polarizable electrodes, convenient forms of which, known as diverting vessels and diverting cylinders, are represented in Figs. 278 and 279, and by which no currents are generated when nerve or muscle is placed in contact with the same. A diverting vessel (Fig. 278) consists of a zinc trough (T), containing a saturated

FIG. 278.



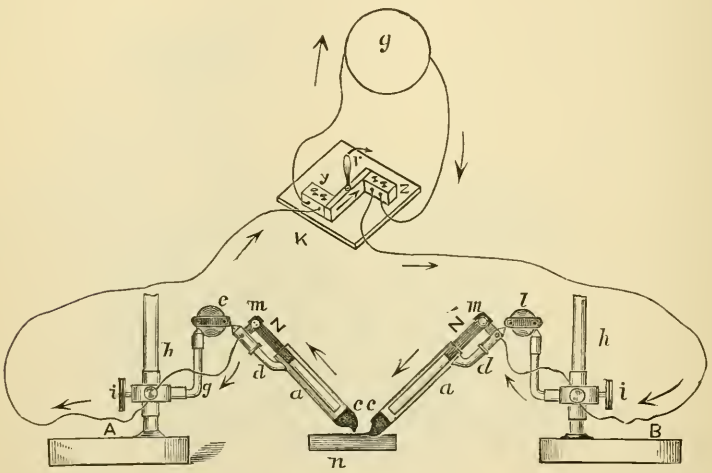
Homogeneous diverting vessel.

solution of zinc sulphate, the inner surface of the trough being carefully amalgamated, and the outer surface coated with a layer of black varnish, the object of the latter being to prevent the sulphate solution coming in contact with any unamalgamated zinc.

It may be mentioned incidentally in this connection that the amalgamating fluid used is that known as Bergot's, prepared by dissolving at a gentle heat 200 grammes of metallic mercury in a 1000-gramme mixture consisting by weight of one part of nitric acid to three parts of hydrochloric acid, and adding then 1000 grammes of the latter acid. The fluid should be kept in a cool, dark place, to avoid decomposition. The trough, insulated by a base of vulcanite (V), and provided with a binding screw (K), can be lifted by a handle (R). The insulated cushions (C), called deriving cushions, are made up of a series of layers of white Swedish

filtering paper, which are stitched together at one end to secure them, and their sides cut perpendicularly with a sharp razor, and soaked in the zinc solution and squeezed so as to get rid of the bubbles of air which would offer resistance to the current. These cushions fill up the cavity of the trough, and project over the lip of the latter, a plate of ebonite (E), and an Indian-rubber band (B) retaining the cushion in this position. Inasmuch, however, as the nerve to be examined, if placed directly upon the deriving cushion would be corroded by the zinc sulphate solution in which the cushion has been soaked, a guard (G) is made, consisting, as already mentioned, of china clay worked up into a soft mass with a 0.5 or 1 per cent. solution of sodium chloride, which when freed of bubbles of air and flattened into a sheet (G) is folded over the

Fig. 279.



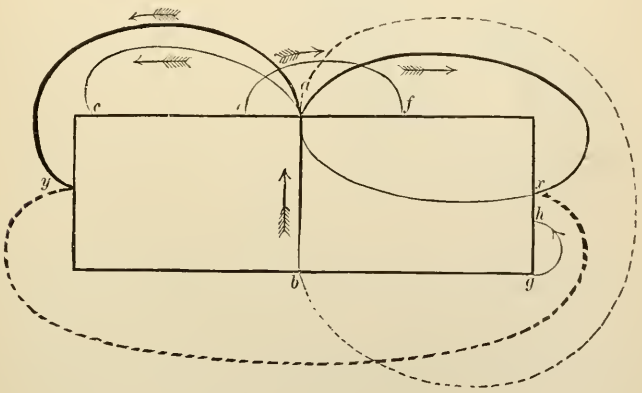
Diverting cylinders.

cushion. A small piece of mica may also be placed upon the clay guard to limit the part to be touched by the tissue. The clay guard not only prevents the corrosion and destruction of the nerve, but through the presence of the salt, the secondary resistance, which would otherwise arise between the liquid conductor and the tissue, and diminish the intensity of the current to be examined is avoided, the salt at the same time being a good conductor. Two diverting vessels being so prepared, a fine silk-covered copper wire is carried from the binding screw (K) of one of the troughs (T) to one side of the Du Bois Reymond key, and another wire from the other trough (T′), not represented, to the other side of the key, wires being also carried from the key K to the binding screws of the galvanometer *g*, as in Fig. 279. Such being the disposition of the diverting vessel, the key and galvanometer, if the key be down,

the diverting vessels are short-circuited, but if up, are in communication with the galvanometer. Finally the troughs can be directly connected together by approximating them or indirectly by a closing cushion made out of blotting paper saturated in the zinc solution, etc., like the deriving ones. The diverting vessels, key, and galvanometer being so disposed before performing any experiment, it ought to be first shown that the diverting vessels are homogeneous or non-polarizable. To do this, the key being down, and the needle of the galvanometer at zero, the two diverting vessels are connected together, and the key opened; if the needle still remains at zero we may be assured that there is no electrical current, that the diverting vessels are homogeneous or non-polarizable.

Apart from the fact that the nerve whose electricity is to be examined cannot always be placed between the cushions in the position desired, it is also often impossible to bring particular points of the nerve in contact with the latter. We frequently, therefore, make use of the non-polarizable electrodes represented in Fig. 279, known as diverting cylinders, which consist of a flattened tube of glass (*a*) mounted on a universal joint (*m l*), and supported on a brass upright (*h*) closed at one end (*c*) by moistened china clay and filled with the saturated zinc sulphate solution in which is immersed the slip of amalgamated zinc Z. The clay (*c*) projecting from the end of the tube can be sharpened into a point so that any two parts of the nerve can be touched that is desired. That no polarization occurs when the points of such electrodes are placed in contact with the nerve is shown by the absence of the products of electrolytic action which would otherwise accumulate at the electrodes.

FIG. 280.



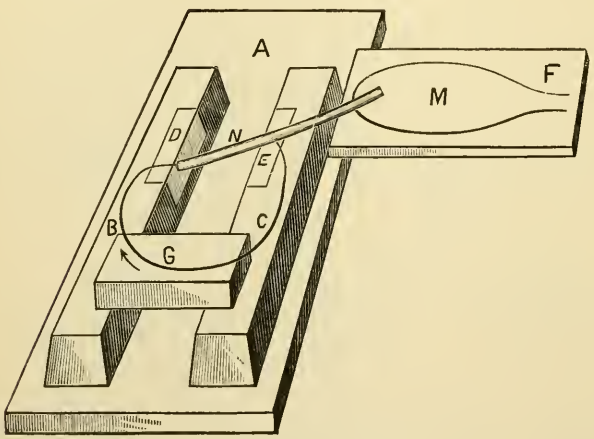
Electrical currents of nerve.

Such electrodes are not only serviceable in diverting an electrical current from the nerve to the galvanometer, but can be also used for the purpose of stimulating a nerve by electricity in the same manner as already described. The deriving cushions (Fig. 278), or

the diverting cylinders (*a*), and the key (K) and galvanometer (*g*) having been connected as represented in Fig. 279, and a freshly prepared nerve (*n*) having been placed upon the cushions or in contact with the points of the cylinders so that its transverse section or cut end is in contact with one of the cushions or cylinders, and its longitudinal uninjured surface at the equator with the other, with the opening of the key the needle of the galvanometer will at once be deflected, and in a direction which shows that the electrical current in the nerve passes, as indicated by the arrows (Fig. 280), from the longitudinal surface of the nerve (*a*) through the galvanometer to the transverse cut surface (*x y*), the remainder of the circuit being completed by the nerve itself. In this connection it may be mentioned that the galvanometer is not indispensable, if we wish simply to demonstrate the electrical nerve current, as it may be accomplished by what is known as the physiological rheoscope, which is prepared in the following manner:

Upon an insulated glass plate A (Fig. 281) are placed two pieces of blotting paper (B C) soaked in salt solution, which support two

FIG. 281.



Physiological rheoscope.

albuminous guards (D E), upon which rests the nerve (N) of a nerve-muscle preparation, the cut end of which is in contact with the pad D, the longitudinal surface with the pad E, the muscle (M) being supported by the glass plate F, also insulated.

The nerve being so disposed, with the alternate connection and disconnection of the two pieces of blotting paper (B C) by a third piece (G), the muscular contraction that follows in both instances indicates the presence of an electrical current in the nerve passing in the direction of the arrows.

Returning now to the case of the nerve when in connection with the galvanometer (Fig. 280), and experimenting a little further by

changing the position of one or both of the electrodes, it will soon be learned that while the current always passes from the longitudinal to the transverse cut surface, the amount of the deflection of the galvanometer needle varies very much according to the position of the electrodes. In certain positions, indeed, as where the electrodes are placed on different sides of the nerves exactly opposite to each other (*a b*), or on points equidistant from the equator (*e f*), the needle is not deflected at all, there being no difference of electrical potential at such places. Such was also supposed to be the case with reference to the ends of the nerve. It has been shown, however, by Du Bois Reymond and Mendelssohn[1] that a current passes through the nerve from transverse section to transverse section, to which the name of "axial stream" has been given by these observers. On the other hand, if one electrode remaining at the cut surface, we move the other along the longitudinal surface toward the equator the deflection of the needle will be increased, the maximum being reached when the electrodes are at the equator of the longitudinal and transverse surfaces, as in the experiment represented in Fig. 280, *a b*. Experimentally, in this way, with the galvanometer, it may be learned that all parts of the longitudinal surface of any nerve are positively electrified with reference to the transverse cut surface, and that if any two points (*e f*) of the longitudinal surface, that nearest the equator of the nerve (*e*) is positively electrified with reference to that more distant (*f*).

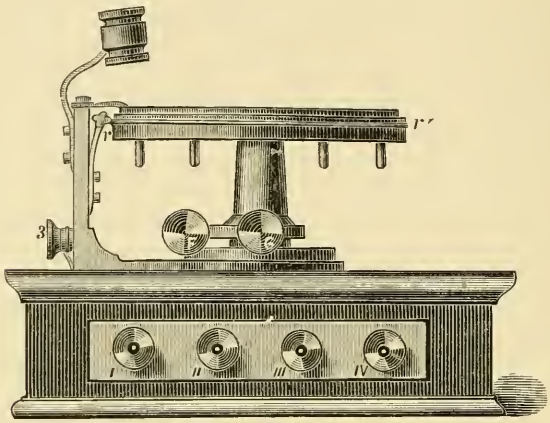
That a similar relation exists between the equator of the transverse cut surface and its periphery, though not experimentally demonstrated, is rendered highly probable from the fact of such a relation having been demonstrated in the case of muscles, as we shall see hereafter. Further, by experimenting with different nerves it will be found that the length and thickness of the nerve influence the amount of the electrical current, it being greater in long, thick nerves than in short, slender ones. That an electrical current exists in the nerve during a state of rest, there can be after what has been said, no doubt, whatever the subsequent explanation of the phenomena may be; but it must be admitted, and the admission is an important one as regards any inference to be hereafter drawn as to the relation between nerve electricity and nerve force, that in an uninjured nerve, in which no transverse section has been made, there is no evidence of an electrical current, that is to say, the nerve is isolectric.

The electro-motive force of nerve currents such as those just described can be determined by means of a galvanometer and round compensator (Fig. 282), the principle made use of being essentially the same as that by which a body is weighed. The method consists in shunting off by means of the compensator (Fig. 283, III), from the circuit of a standard element, a Daniell cell (D), for ex-

[1] Ueber den axialen Nervenstrom, Maurice Mendelssohn, 1885, Archiv f. Anat. und Phys. separat-abdruck.

ample, whose electro-motive force is known (1.08 volts), an amount of current sufficient to neutralize or compensate the current deflecting the magnet due to the electro-motive force of the nerve N, which is to be determined, just as the unknown weight of a body is learned

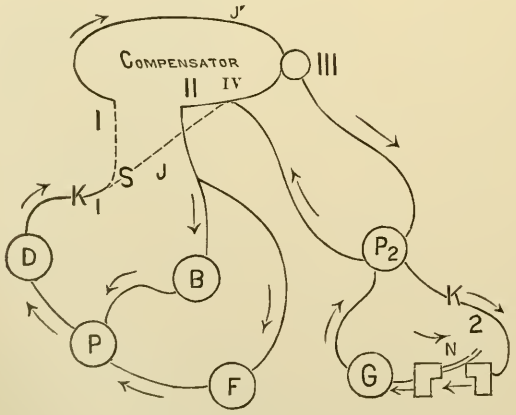
FIG. 282.



Du Bois Reymond's round compensator.

from the known weight necessary to neutralize or balance it. Let us suppose that the electrical current diverted by the now polarizable electrodes from the nerve N, the sciatic of the frog, for example, to the Wiedemann galvanometer G, be sufficient to deflect the magnet to an extent corresponding to 25 divisions of the scale. If

FIG. 283.



Schema for determining electro-motive force by round compensator.

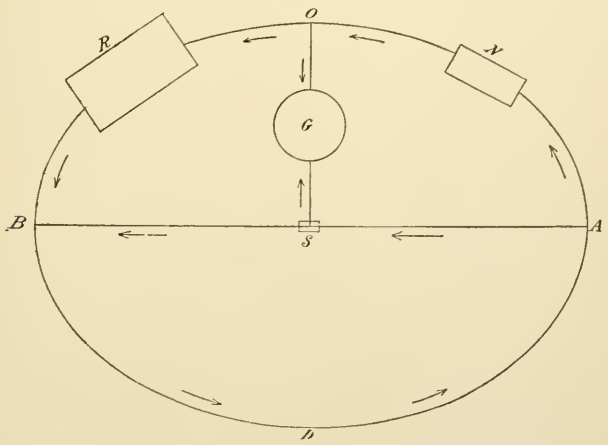
now the compensator be turned until the wheel reaches III, part of the current from the Daniell cell will return through IV, II, F, whence it came, and part through III, P_2 to the nerve N, and be-

ing in the reverse direction to the current due to the nerve the magnet will be brought back to zero. Such being the case it follows that the electro-motive force of the nerve current is equal to that shunted off from the compensator and neutralizing it, and which amounts, the wheel being at III, to the $\frac{1}{50}$ of a Daniell or 0.02 volt.[1]

Recent researches[2] have shown the electro-motive force of the currents in the nerve and spinal tracts of the cat to be 0.01 and 0.04, and in the corresponding parts in the ape 0.005 and 0.29 of a Daniell cell respectively. According to Mendelssohn[3] the electro-motive force of the axial current of the posterior roots of the spinal nerves of frogs—that is, of the current from equator to central or peripheral transverse section amounts respectively to 0.00893 and 0.00767 of a Raoul, that element (copper in copper sulphate solution, and zinc in zinc sulphate) being used instead of a Daniell.

As the electrical current of a nerve, after passing through a galvanometer, must, in returning to the point from which it started, pass through the nerve, and as induced and constant currents are

FIG. 284.



Schema for determining the resistance of nerve.

frequently thrown into a nerve, the resistance offered by the latter to the passage of an electrical current must also be determined. This is accomplished by essentially the same method as ordinarily made use of in determining the amount of resistance offered by bodies in general to the passage of electricity, and is briefly known as that by the Wheatstone bridge. This method is based upon the

[1] For the method of determining this, as well as for the construction and manner of using the compensator, the reader is referred to "Researches upon the general physiology of nerve and muscle," No. 1, by H. C. Chapman and A. P. Brubaker, Proc. of Acad. Nat. Sciences, Phila., 1888, p. 106.

[2] Gotch and Horsley, Phil. Trans., Vol. 182, 1891, pp. 267–526.

[3] Op. cit., s. 387.

principle of so disposing the body whose resistance is to be determined, that the current of electricity traversing it passes through a galvanometer in an opposite direction to that traversing a body whose resistance can be varied, until the current traversing the body exactly neutralizes the former current, as shown by the galvanometer's needle remaining at zero.

Such being the case, the unknown resistance is then equal to the known one; otherwise there would be a deflection of the magnetic needle according as the one body would offer a greater or less resistance to the current than the other. Thus, supposing that the apparatus be arranged as in Fig. 284, then the current from a Daniell's element D, on arriving at A, the end of the long wire $A\ B$, or rheocord, splits into two branch currents, one of which will traverse the body N, a nerve, for example, whose resistance is to be determined, and the other the wire $A\ B$. Further, the first branch current, on arriving at O, will divide into two, one of which will pass into the resistance box R, the other into the galvanometer G; the latter current being opposite in direction to that coming from S, one of the two branch currents into which the current $A\ S$ divides, the remaining one passing from S to B, and thence back to the Daniell's element. But, as the resistance offered to the current passing from A toward B can be increased or diminished by the sliding of S from or toward A, all the current returning to the battery when the slider is at A, by varying the position of the slider a point will be reached on the wire, as at S, when the galvanometer needle will remain at zero, showing that the current passing down from the nerve from O to the galvanometer is equal and opposite in direction to that passing up from the wire at S. Such being the case, then the resistance offered by the nerve, or x, is to that of the resistance box R, as the part of the wire $A\ S$ is to the part $S\ B$—that is, $x : R :: A\ S : S\ B$. Now, as the resistance R is learned by observing the number of plugs out, and that of $A\ S$ and $S\ B$ being also known, the rheocord wire having been previously graduated, the unknown resistance of the nerve, or x, is given in terms of R, $A\ S$, and $S\ B$, as shown by the equation

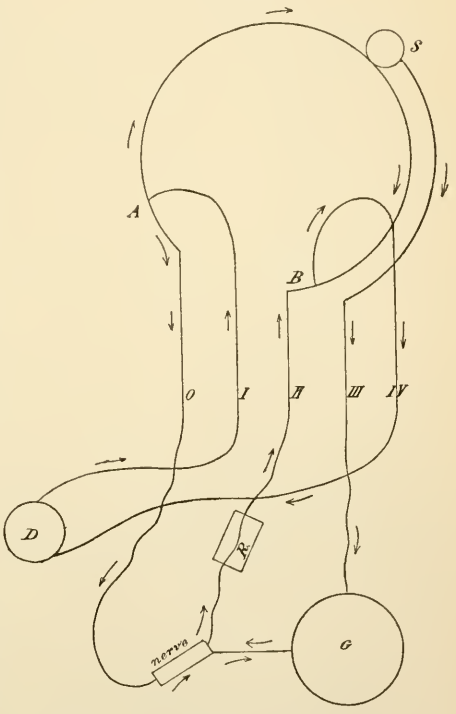
$$x = \frac{R \times AS}{SB}.$$

If $A\ S$ and $S\ B$ be constant and equal, then the resistance offered by N equals that of R, and can be inferred directly from the latter.

The method just described of determining the resistance offered by a nerve, for example, to the passage of a current of electricity is at times inconvenient, even quite awkward, on account of the length of the rheocord wire involved. For this reason we make use of the round compensator (Fig. 285) with, however, the accessory binding screw O. The principle of determining the resistance, it is needless to add, however, is not at all affected by this modification for determination of resistance of nerve, the difference be-

tween the long and round rheocord or compensator being simply in the disposition of detail. Thus, if Fig. 285, a schematic representation of the round compensator, be compared with that of Fig. 284, the long one, it will be observed that in both instruments the current from the Daniell's element D, on arriving at A splits into two currents, one of which passes to the wheel or slider S, the other to the nerve; that the current at S divides into two, one of which passes to the galvanometer G, the other back to the Daniell's element; that the current after traversing the nerve divides into two, one of which passes to the galvanometer G, the other to the resistance box R, and thence back to the Daniell's element; that the two currents, passing in opposite directions through the galvanometer neutralize each other. It follows, therefore, that in using the modified round compensator we obtain the same proportion as in using the long one, viz.:

Fig. 285.



Schema of round compensator, with modification.

$$x : R :: AS : SB,$$

$$\text{or } x = \frac{R \times AS}{SB}.$$

The value of x, or the resistance of the nerve, as obtained by this method, we have determined to be in a portion of the sciatic nerve of the frog, 2 cm. long, 1 cm. broad, and 0.5 mm. thick, when exerted longitudinally, twelve million times greater than mercury when taken as unity, and when transversely thirty-two million times greater.[1]

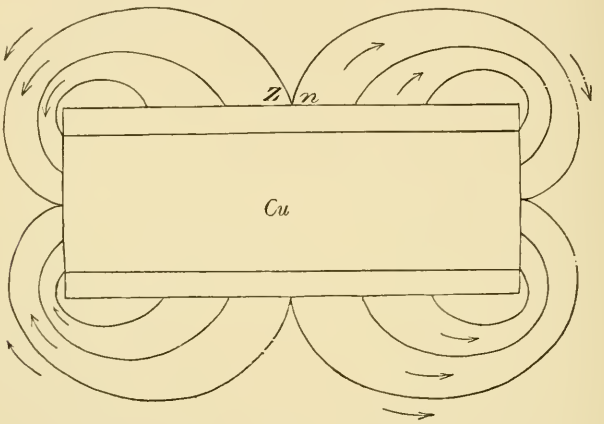
It may be mentioned in this connection that while the resistance offered by the human body to the passage of an electrical current is very great in a state of health, it appears to be diminished in certain kinds of disease, so much so in Grave's disease, for example, as to constitute an important diagnostic symptom.

Having considered the nerve current and the electro-motive force of the nerve, and the resistance offered by the nerve to the passage

[1] Researches upon the General Physiology of Nerve and Muscle, No. 2, by H. C. Chapman and A. P. Brubaker, Proc. Acad. Nat. Sci. Phil., 1888, p. 155.

of electricity, it remains for us now to offer, if possible, some explanation of the natural nerve current based upon its physical structure. It is well known that if a solid copper cylinder (*Cu*, Fig. 286), covered except at its ends by a layer of zinc, *Zn*, be immersed in a conducting fluid like water, that electrical currents are developed, which, as may be shown by the galvanometer, pass from the longitudinal or zinc surface to the transverse copper one, and

FIG. 286.



Apparatus for the development of electrical currents.

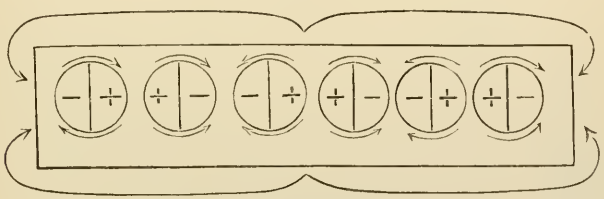
that, according as the electrodes are shifted from point to point of its copper and zinc surfaces, these currents become stronger, weaker, or disappear altogether, and that while if the copper be entirely covered by its zinc mantel there is no appreciable electrical current, however the electrodes may be placed. When it is remembered that the ultimate nerve fiber consists histologically of the axis-cylinder surrounded by the white substance of Schwann and neurilemma, it might appear at first sight that one or the other of these two membranes bears to each other, or to the axis-cylinder, the same relation electrically that we have seen the outer zinc mantel does to the copper axis of the simple physical apparatus just described.

That such, however, is not the case, is proved by the fact that even at the nodes of Ranvier in the spinal nerves, and in the sympathetic fibers also, where the white substance of Schwann is absent, nevertheless, electrical currents can be shown to exist, evidently then it cannot be the contact of the substance of Schwann with either the neurilemma or the axis-cylinder that is the cause of the difference in the electrical potential, while the presence of electrical currents in the cord in the absence of the neurilemma equally shows that the contact of that membrane with the axis-cylinder has nothing to do, any more than the white substance of Schwann, with the development of such currents. The only conclusion to be drawn

from such facts is that of the three parts of which the nerve consists, it is the axis-cylinder only which is concerned in the development of the electrical current, and which confirms the conclusion that we have come to upon other grounds that the axis-cylinder is functionally the most essential part of the ultimate nerve fiber. Among the many theories that have been offered as explanations of the presence of electrical currents in nerves, it has been held for example that the electrical current developed in a nerve in which a transverse section has been made, is due to the fact that the negatively electrified axis-cylinder is then exposed to the positively electrified nutritive fluid surrounding it, since, as we have just seen, the difference between the longitudinal and cut surfaces electrically cannot be attributed to the contact of either neurilemma or substance of Schwann with the axis-cylinder. If such be the case, it becomes intelligible why, as we have already mentioned, there is no appreciable electrical current in the uninjured nerve—that is, in one without a transverse cut section, since under such circumstances the negative axis-cylinder is not exposed to the positive nutritive fluid surrounding the nerve, just as in the case of the physical apparatus (Fig. 286) there is no electrical current developed as long as the negative copper axis or core is completely enveloped by the positive zinc mantel or hull.

As an illustration of the influence of the contact of a surrounding fluid upon a tissue in the development of an electrical current, it may be here mentioned that if the transverse cut surface of a dried muscle be placed upon the surface of distilled water, that an electrical current will be developed, passing from the longitudinal to the cut surface as soon as the muscle begins to swell through imbibition of the fluid with which its transverse section is in contact. While the explanation just offered, that of Gruenhagen,[1] was consid-

Fig. 287.



Electromotive double dipolar molecules.

ered by that physiologist as satisfactorily explaining the electrical condition of the cut nerve, however plausible it may appear, it must be mentioned that it is not generally accepted by physiologists. Thus, Du Bois Reymond[2] for many years held that the nerve consists

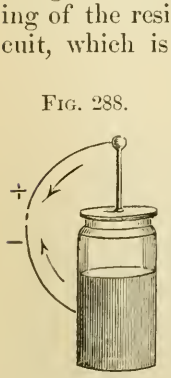
[1] Funke, Physiologie, Erster Band, 1876, s. 487.

[2] Untersuchungen über Thierische Electricität, Zweiter Band, s. 323. Berlin, 1849.

not of a homogeneous axis, surrounded by a hull like that of the physical apparatus just described (Fig. 286), but of a series of electro-motive double dipolar molecules, imbedded in an indifferent and imperfectly conducted medium (Fig. 287), each double molecule consisting of a positive and negative part, the two positive parts placed together within, the two negative parts without, the double molecule presenting then a negative surface at the transverse section or cut end, and a positive surface at the longitudinal surface of the nerve. Regarding the double molecule as a minute battery whose positive and negative poles are at the longitudinal and transverse surfaces, respectively, currents will be developed which through the imperfect conductility of the medium will circulate in more or less eccentric lines not only in the immediate neighborhood of each molecule, but at some distance from the latter, from the positive middle surface to the negative ends of the nerve as indicated by the arrows, and giving rise to the deflection of the galvanometer needle, as we have seen is the case when the electrodes are applied to the nerve. Suppose that the nerve does consist according to this hypothesis of molecules, such as just described, it is evident that the electrical current within it is a closed one, the nerve differing in this respect from the zinc-copper apparatus as regards any current diverted into the galvanometer. In either case the current can only be a partial one, the deflection of the needle indicating the presence of a current, but in no wise the total strength of the current due to the electro-motive force of all the molecules.

That the strength of the latter must be much greater than the partial current deflecting the needle is shown by the necessity of using such sensitive galvanometers, and is implied in the overcoming of the resistance both of the nerve and the galvanometer circuit, which is considerable. Indeed, were not the total electric strength of the molecules much greater than that of the partial current, the latter would not be appreciated by the galvanometer at all. It is for such reasons that Du Bois Reymond holds that the electro-motive force of the nerve molecules exceeds that producing all other known currents, and is capable, in the highest degree, of producing all the known effects of currents. While there is much to be said in favor of Du Bois Reymond's view of the nerve consisting of electro-motive molecules, it must be admitted that it is difficult to explain on such a theory the weak currents that are developed by placing the electrodes upon different points of the longitudinal surface, and why currents of any kind are only present in the injured nerve, or one presenting a transverse section. Indeed, this latter fact, equally an objection to the view offered by Gruenhagen, has led physiologists, like Hermann,[1] to deny alto-

Fig. 288.



Leyden jar.

[1] Handbuch, Zweiter Band, Erster Theil, s. 169. Leipzig, 1879.

gether the preëxistence of any electrical current in the nerve, attributing the latter to the death of the transverse cut surface, which, at that moment, becomes negative to the longitudinal surface. On the other hand, according to Radcliffe,[1] the electrical character of the nerve current is rather static in its nature than voltaic, the nerve being compared on this view to a charged Leyden jar (Fig. 288), the current being simply accidental, and due to the applying of the electrodes of the galvanometer to points having different electrical tensions. After all, however, the difference between static and voltaic or current electricity is not a profound one, being rather one of degree than of kind, since the former is one of high tension, but small in quantity, the latter of low tension, but large in quantity; by tension being meant the tendency of the electricity accumulated at the extremities of the electrodes to free itself.

[1] Dynamics of Nerve and Muscle, p. 24. London, 1871.

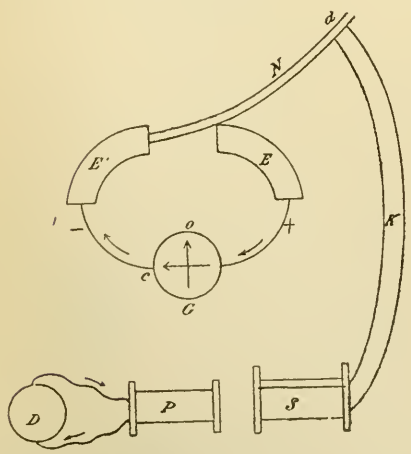
CHAPTER XXIX.

THE NERVOUS SYSTEM.—(*Continued.*)

CURRENTS OF REST AND OF ACTION. NEGATIVE VARIATION. ELECTROTONUS. ELECTROTONIC MODIFICATION OF EXCITABILITY.

WHATEVER view may be held as to the nature and cause of the electrical current present in an injured nerve during rest, there is no difference of opinion as to the fact that it is diminished during activity. The deflection of the galvanometer needle in the latter case is accounted for, however, by Du Bois Reymond, on the supposition that the current of rest undergoes during activity a diminution, a "negative variation," while according to Hermann, and most physiologists, it is due to the development of an "action current," independent of and in a direction opposite to that of the current of rest. That the negative variation or action current constitutes an essential feature of nervous action, is shown from the intensity of the one varying with the other, and, as already mentioned, from the rate at which it travels along the nerve being the same as that at which the nerve impulse itself is propagated. While the current of action or negative variation can be shown by stimulating the nerve with a single induction shock the phenomenon becomes much more evident when the induction apparatus is used with the automatic interrupter, since the shocks thrown into the nerve succeed each other so rapidly that before the galvanometer needle can return to its first position, that due to the current of rest, it is again deflected by the negative variation or current of action and consequently remains in one position, that due to the latter. Thus, for example, suppose that the transverse section of the nerve N be in contact with one of the diverting electrodes E' (Fig. 289), and the longitudinal surface with the other, and that

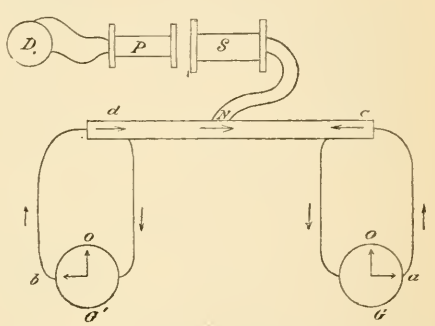
FIG. 289.



Disposal of apparatus to show the current action or negative variation.

the deflection of the magnetic needle at G, due to the current of rest, amounts to, say C. Such being the case, if now the nerve N be stimulated by the induction apparatus, the deflection of the needle in the reverse direction back towards zero, o indicates either the presence of an "action current" or that the current of rest has been diminished, has undergone a negative variation. If now the experiment be so modified (Fig. 290) that while the nerve is stimulated in the middle N, its two ends (c d) are in contact with the electrodes of two galvanometers (G G'), it will be observed that there is a current of action or a diminution in the current of rest ($a - o$, $b - o$) of the nerve at both ends, showing that the disturbance in the electrical condition of the nerve, whatever its nature may be, is propagated in both directions, from the center or the point of the application of the stimulus: a very important fact, since, if the current of action or the negative variation is intimately associated with that of the development and propagation of the nerve impulse, it proves that the latter is transmitted from the point of stimulus, both to the central and peripheral ends of the nerve, confirming the view already advanced, that the nerve impulse is transmitted in both directions and that the function of a nerve depends, not upon its intrinsic structure, but whether it terminates in a motor, sensory, or glandular organ.

FIG. 290.

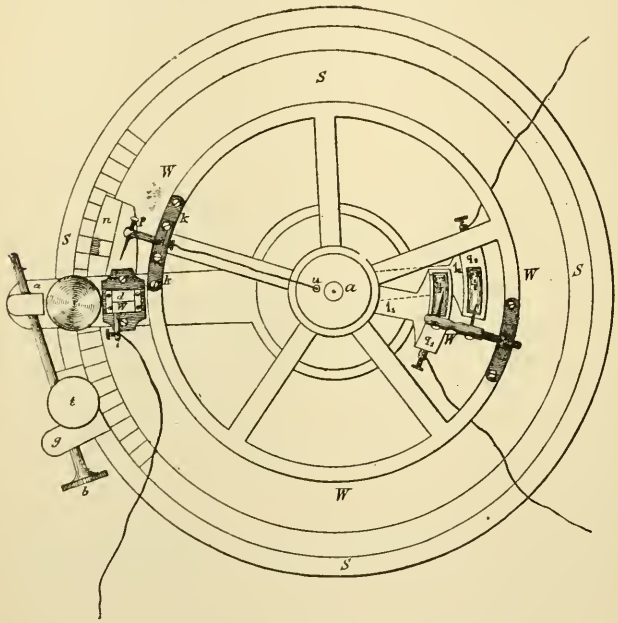


Disposal of apparatus to show that the current of action or negative variation is transmitted in both directions.

By extending our experiments it will be further found that all kinds of nerves, motor, sensory, secretory, exhibit the phenomena of negative variation, the amount of the latter at different points of the nerve depending, however, upon that of the preëxisting current of rest. If, however, the latter be absent, there will then be no negative variation though there may be currents of action independent of the latter. Thus, if the diverting electrodes be placed upon two points of the longitudinal surface symmetrically disposed with reference to the equator, the magnetic needle not being then deflected by the nerve current, there can be no diminution of the latter or negative variation. An interesting fact as regards the phenomenon of negative variation is, that it cannot only be produced by artificial stimuli, electrical, chemical, thermal, and mechanical, but by natural ones inherent in the nervous system itself by stimuli from the spinal cord, for example. Thus it is well known that if the sciatic nerve of a living frog be well exposed,

avoiding, however, the injuring of the blood vessels and the origin of the nerve, and the nerve be cut through at the popliteal space, and the electrodes so disposed that the point of one is in contact with the equator, and the point of the other with the cut surface of the nerve, that with the appearance of the muscular cramps due to the subcutaneous injection of strychnia, the electrical current of the nerve will undergo a negative variation. The significance of this experiment will be better appreciated, however, when the subject of reflex action has been considered; since the muscular contraction in strychnia poisoning is due to an impression made upon the skin and transmitted to the spinal cord, and thence reflected by the spinal nerves to the muscles.

Fig. 291.



Bernstein's differential rheotome. Horizontal view.

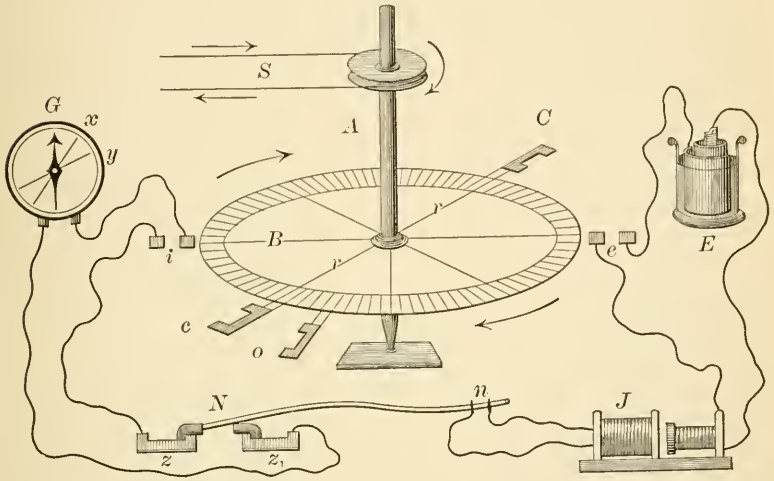
Negative variation occurs also during the tetanus brought about by the mechanical crushing of a nerve, the destruction of the latter by heat, or when induced by the stimulation of cutaneous branches, as in the case of the sciatic nerve, for example.

Recent researches[1] have shown, when electrodes connected with a capillary electrometer are applied to the motor tracts of the spinal cord, spinal nerve roots, or peripheral nerves, that with stimulation of the cortical motor areas, the currents of rest present, undergo negative variation, or are neutralized by currents of action. It

[1] Gotch & Horsley, Phil. Trans., Vol. 182, 1891, pp. 267–526.

has already been mentioned that the rapidity at which the negative variation is transmitted is the same as that of the nerve impulse itself. This was first determined by Bernstein[1] by means of his differential rheotome (Fig. 291). The principle of this instrument (Fig. 292) consists in closing, by *C* at *c*, the primary circuit

FIG. 292.



Schema of Bernstein's differential rheotome. *N n*. Nerve. *J*. Secondary coil of induction machine. *G*. Galvanometer. *x*, *y*. Deflection of needle. *E*. Battery. *C* closes primary circuit at *c*. *c* closes galvanometer circuit at *i*. *z z*. Electrodes in galvanometer circuit. *S*. Cord from motor. (LANDOIS.)

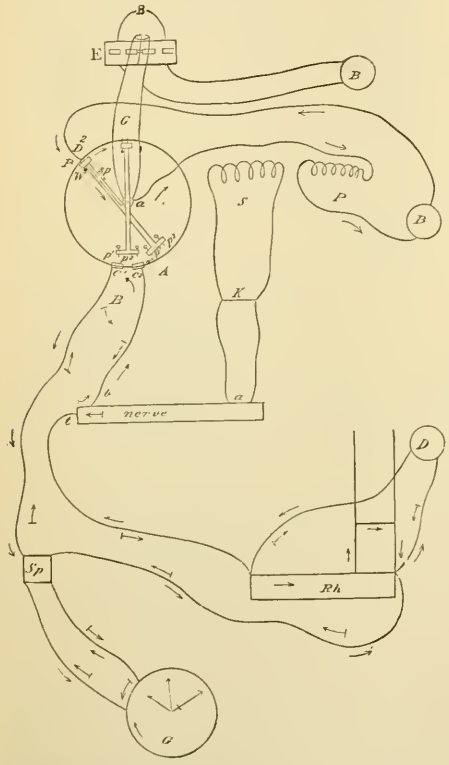
stimulating the nerve through *J*, and that diverting its current of rest, by *c* at *i*, by a wheel, rotating at a known rate, and of so disposing the two pairs of electrodes that the stimulating circuit is closed before the diverting one, the interval of time elapsing between the two—that is, the time during which the nerve impulse passes from *n* to *N*—being determined from the rate at which the wheel is rotating.

To explain the manner in which the rapidity of the propagation of the negative variation is determined, in the frog for example, by means of the differential rheotome, we will begin at the moment that the rotating wheel *C* (Fig. 292) comes in contact with *c*. At that instant the primary circuit is closed and the nerve being stimulated by *J* at *n*, the current of action or negative variation will begin at that point and will be transmitted to the other end of the nerve *N*, the wheel coming in contact however at that instant through *c* with *i* and the galvanometer circuit being then closed, the needle will be deflected in an opposite direction to that due to the current of rest, the latter having undergone negative variation. As the current of action or negative variation is transmitted through the nerve from

[1] Untersuchungen über den Erregunsvorgang im Nerven- und Muskel-systeme. Heidelberg, 1871.

the point of application of the stimulus at n to that of the diverting electrodes at N, and as the deflection of the galvanometer needle occurs at the moment that the diverting circuit is closed, the rate at which the current of action or negative variation is propagated becomes known since it is transmitted from n to N in the same time that c moves to i, C having first reached e, that is at the rate of 28 meters per second. It was at one time supposed that the current of action or negative variation occurs during the latent period, and during its transmission through the nerve, preceded the nerve impulse. It is more probable, however, that the two movements accompany each other, as it has been shown that the current of action or negative variation that occurs in muscle, accompanies the contraction wave of the latter[1] and which corresponds to the impulse in the nerve.

Fig. 293.



Disposal of differential rheotome, etc., for determination of rapidity of propagation of the current of action or negative variation.

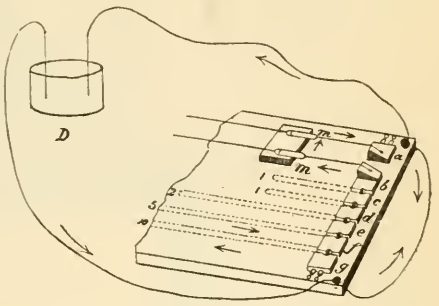
It will be seen from the disposition of the apparatus represented in Fig. 293 that the current of rest is compensated by means of the Daniell cell and rheocord. The galvanometer needle will remain, therefore, at zero until the current of action or negative variation reaches the end of the nerve t, when the needle will be deflected by it, and in the opposite direction to what it would have been deflected by the current of rest had not the latter been compensated.

The object of so compensating the nerve current in the study of its negative variation by means of the differential rheotome is that the movement of the needle should always begin at the same point, viz., zero. It will be noticed, however, that the rheocord—that of Du Bois Reymond—differs in its form from that previously described, though the latter, for the present purpose, might have been just as well used. The rheocord (Fig. 294), consists of a long box, at the edge of which are stretched two platinum

[1] Burdon Sanderson, Proceedings of Royal Society, 1890.

wires, passing through the connected mercury cups *m m*, which can be pushed to the other end of the box along the scale graduated in millimeters at the side. When the mercury cups are directly in contact with the brass *a*, the resistance offered by the rheocord to the Daniell's circuit is practically nothing as compared with that offered by the nervous circuit, consequently the current from the Daniell's element simply passes through the rheocord back to the cell, none being diverted into the nervous circuit. If, however, the mercury cups be pushed away from the brass along the platinum wires, the wires offering a resistance, the amount indicated by the scale, 358 mm. = 1 ohm, and there being no passage for the current from one side of the rheocord to the other, except through the parts of the wires lying between the mercury cups and the brass, it follows that a proportional part of the total current from the Daniell's element is thrown into the nervous circuit.

Fig. 294.



The rheocord.

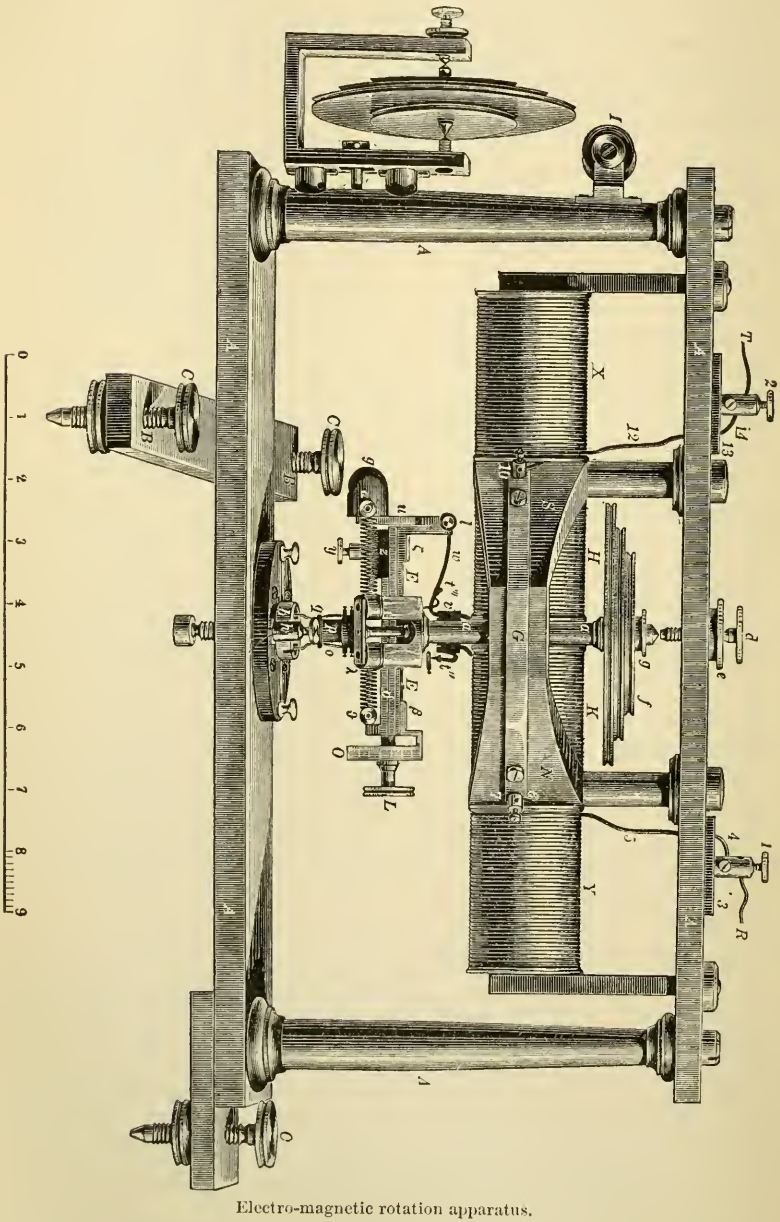
If a greater amount of resistance is needed than that obtained by pushing the mercury cups through the whole length of the platinum wires, then the plugs lettered *b, c, d, e, f, g*, or numbered, can be drawn out, these being multiples of the resistance offered by the total length of the platinum wires traversed by the mercury cups, the amount of current thrown into the nervous circuit will be then proportionally increased. Thus, for example, if the plug 5, letter *g*, be withdrawn, then the amount of current thrown into the nerve will be five times as great as when the mercury cups were at the end of the wire, and so proportionally for the remaining plugs. In fact, the rheocord is a form of resistance box, such as already described.

The wheel of the differential rheotome, as has already been mentioned, is uniformly rotated by the electro-magnetic rotation apparatus of Helmholtz (Fig. 295, *E*). The latter consists of four electro-magnets, the two external ones (*X X'*) immovable, the two internal ones (*H K'*) movable; the latter are fixed to the axis by their dissimilar poles, and are supplied by three Daniell's elements, the external ones by one. As the two internal magnets are repelled and attracted by the external ones, the axis is rotated, and with it the wheel, through which it passes, and around which passes the thread from the disk of the rheotome.

Although the phenomenon of the negative variation is a momentary one its duration has been determined by means of the rheo-

tome to amount to 0.0007 second. Such being the case it follows that during the 0.0006 or 0.0007 second that the point a of a

FIG. 295.

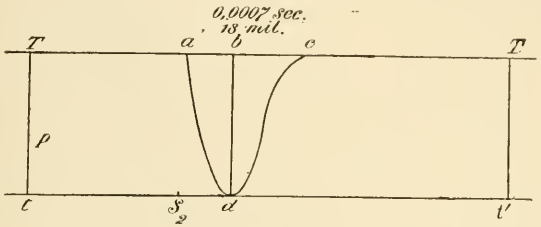


Electro-magnetic rotation apparatus.

nerve (Fig. 296) undergoes its negative variation the intermediate points between a and c will be successively affected in the same

way, the point c passing into the condition of negative variation at the end of the 0.0006 or 0.0007 second as the point a passes out of it. The negative variation is propagated, therefore, in the form of a wave, and, being at the rate of 28 meters a second, the wave must be 18 mm. long. That is to say, if the current of

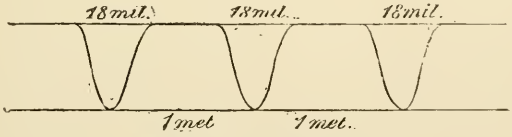
FIG. 296.



Wave of negative variation.

action or negative variation travels along the nerve 18 mm. in from 0.0006 to 0.0007 second it will travel 28 meters in 1 second. Further, if it be supposed that while the negative variation travels at the rate of 28 meters a second, that during the same period of time the nerve be stimulated 28 times, then a nerve 28 meters long would exhibit at the end of the second 28 waves of negative variation, each wave being separated by an interval of 1 meter (Fig. 297).

FIG. 297.



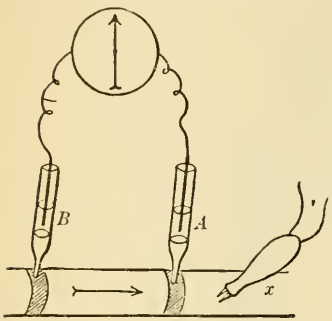
Waves of negative variation.

It having been learned by the rheotome that the current of action or negative variation, produced by successive stimuli following each other periodically, is propagated in the form of a wave of definite length and duration, there can be no doubt that the change undergone by the nerve when in this condition is of a vibratory character. The wave of negative variation or the current of action resembles, therefore, those of water, sound and light, with this difference, however, that in the case of the former chemical changes are probably going on in the nerve substance which are absent in the latter, and of which little or nothing is known.

It has already been mentioned that uninjured nerves are isolectric; that is, do not exhibit electrical currents. If a normal nerve be stimulated, however, a difference of electrical potential at once ensues, and a current flows in the direction of the arrow (Fig. 298) B to A, the part of the nerve first traversed by the impulse becoming negative electrically to the succeeding parts. The current so

developed is of but short duration, and is replaced by one flowing in the opposite direction, A to B, the latter being rendered negative by the passage of the nerve impulse. The current of action in the uninjured nerve is therefore diphasic in character. It will be observed that the currents of action in the uninjured nerve, are produced in the same manner as the currents of rest are supposed by Hermann to be produced in the injured ones in so far at least as one part of the nerve is rendered negative to a succeeding part, in the case of the currents of action, by the transmission of the nerve impulse, in that of the currents of rest by injury. It would appear, however, that while the currents of action of the injured as well as of the uninjured nerves are natural physiological currents, the currents of rest are artificial demarcation currents produced by injury and without functional significance.

FIG. 298.



Stimulation of uninjured nerve. Electrodes at x.

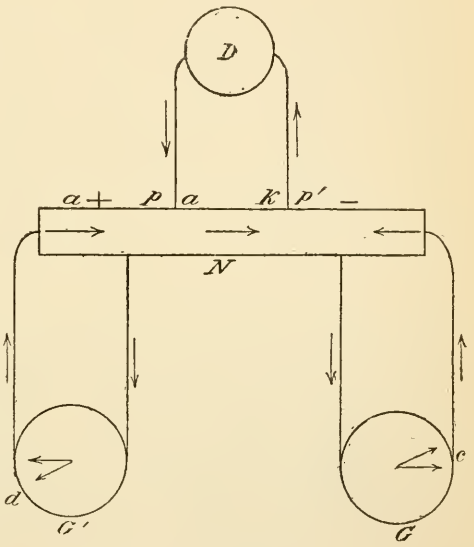
Electrotonus.[1]

Up to the present moment, in exciting the nerve by electrical stimuli we have made use of single or repeated induction shocks, and this not only for convenience' sake, but especially on account of the short duration of induced currents, the object in view being the avoidance of the consideration of the changes undergone by the nerve during the passage of a constant current, and which, had they been present, would have rendered the explanation of the changes due to the induced current a more difficult one. Such changes as are induced in the condition of a nerve through the passage of a constant current passing directly to the nerve without the intervention of an induction apparatus can now, however, be conveniently considered. Let us suppose, then, that N (Fig. 299) represents a nerve, and that through the deviation of the magnets of the galvanometers GG' we learn that the currents of rest are present, passing from the longitudinal surface through the galvanometers to the transverse cut surface of the nerve, through the nerve to the longitudinal surface again in the direction indicated by the arrows. Let now the nerve N be stimulated through the non-polarizable electrodes $p\ p'$ at a point intermediate between its ends, by means of a constant current, say, from a Daniell's element, and which we will hereafter designate as the polarizing current, the deflection of the galvanometer needles will show that the current passing through the galvanometer G' is increased (d) constituting

[1] Du Bois Reymond, Untersuchungen über thierische Electricität, 1848, Band ii., s. 289.

the positive phase, the current through G is diminished (c) constituting the negative phase. It is evident, therefore, that the electrical condition of the nerve is not only modified temporarily by the momentary stimulus of the constant current, but permanently also during the passage of the current through the nerve in the modification of its electrical condition in the manner just mentioned. It will be observed from an inspection of Fig. 299 that the polarizing current is direct—that is, as it passes through the nerve from the anode a, or positive pole, to the kathode k, or negative pole, it flows in the same direction as the nerve force itself. Now if it be assumed that the polarizing current develops outside of the electrodes a k, a new current, the electrotonic current, having the same direction as itself, it is evident that the increasing or diminishing of the currents of rest by the electrotonic current, according as the latter is flowing in the same or in the opposite direction, will account for the difference in the electrical condition of the nerve outside of the anode a, and kathode k, the former being positively, the latter negatively, electrified. Such being the case, we may call that part of the electrotonic current increasing the current the anelectrotonic, that diminishing the same the katelectrotonic current, indicating the electrical conditions of the two currents respectively by the signs plus + and minus —. If now the position of the two electrodes a k be reversed so that the polarizing current flows through the nerve in the opposite direction to that of the nerve impulse, then the anelectrotonic current will be developed at p', the katelectrotonic at p, and the current passing through the galvanometer G will be increased, that through the galvanometer G' diminished. It will be observed, therefore, that the anelectrotonic and katelectrotonic condition just described will depend upon the fact of the polarizing current passing through the nerve in the direct or reverse direction. In either instance, when the polarizing current is broken the currents of rest previously increased or diminished are for a brief moment diminished or increased. It need hardly be added that the electrotonic

Fig. 299.



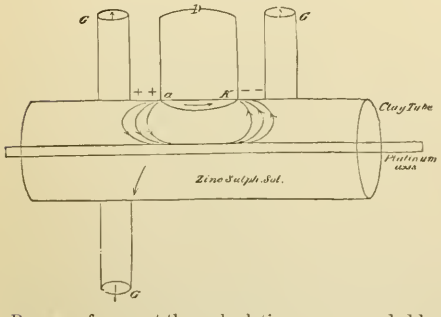
Anelectrotonic and katelectrotonic currents.

currents are entirely independent of the currents of rest, the former being present even when the latter are absent.

By further experimentation it will be found that the strength of the electrotonic currents depends upon that of the polarizing current and of the length of the intrapolar portion of the nerve exposed to the latter, and of the irritability of the nerve, a dead nerve not exhibiting the electrotonic current.

Of the electrotonic currents, the anelectrotonic is of higher potential than the katelectrotonic, the electro-motive force of the former amounting to 0.5 of a Daniell, that of the latter to 0.05 D.[1] The anelectrotonic current differs also from the katelectrotonic current in attaining its maximum and minimum more slowly. It is an interesting fact that both the electrotonic currents undergo a negative variation during the passage of an impulse through the nerve. It may be also mentioned in this connection that the withdrawal of the polarizing current gives rise, through the internal polarization set up in the nerve, to "after currents," the latter being positive, that is, in the direction of the polarizing current when the current is strong, and negative when weak. Considerable difference of opinion prevailed at one time among physiologists as to whether electrotonic currents are due to some especial modification of the electro-motive condition of the nerve, which, like the current of action, is transmitted from the point stimulated, through the nerve, from molecule to molecule, or are due to the direct effect of the polarizing current through an escape of the latter, from the electrodes along the extra-polar portions of the nerve. The latter view is, however, the one usually accepted at the present day as best explaining the facts. At least currents similar to electrotonic ones can be produced when a constant current is transmitted through a conductor consisting, like a nerve, of three parts, such as is represented in Fig. 300, in which the platinum axis represents the axis-cylinder, the zinc sulphate solution the substance of Schwann, and the clay tube the neurilemma. The leaving currents in such a conductor, owing to the substance surrounding the axis being a better conductor than the envelope, will pass from the anode into the former, and thence into the axis, and so return by the latter to the kathode. Further, the electrotonic currents so developed resemble those of a nerve in being entirely dependent upon the polar-

FIG. 300.

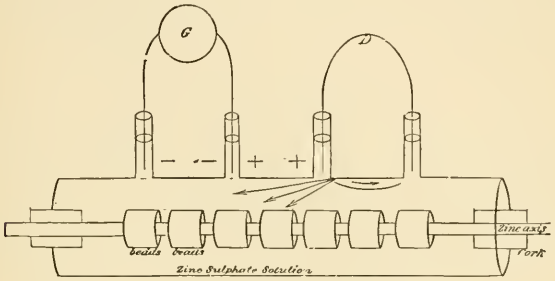


Passage of current through platinum, surrounded by zinc sulphate and clay.

[1] Du Bois Reymond, Gesammt. Abhandl., Band ii., s. 260.

izing current, of the length of the nerve traversed by the latter, etc. If, now, such a heterogeneous conductor be divided in the middle, and the cut ends be joined by a homogeneous moist conductor like that already described, no electrotonic currents will appear for the reasons already given. It is in this way, probably, that the ligation or the crushing of the nerve interferes with the

FIG. 301.

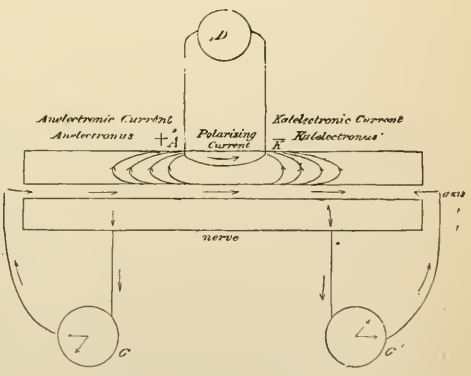


Passage of current through heterogeneous conductor.

development of such currents, the nerve, after death, being changed from a heterogeneous to a homogeneous conductor. Further, as the escape of the polarizing current, either in the nerve or the heterogeneous conductor, appears to be due to the resistance developed through the inner polarization set up between the core and the sheath, it is to be expected that the amount of polarizing current escaping along the extrapolar portions of the nerve will be proportional to such resistance, and such a fact is found to be the case.

An interesting illustration of the difference in effect as regards the development of electrotonic currents due to the conductor being homogeneous or heterogeneous can be readily shown by the following simple apparatus (Fig. 301), which consists of a glass tube through which passes an axis of amalgamated zinc.

FIG. 302.



Passage of current through nerve.

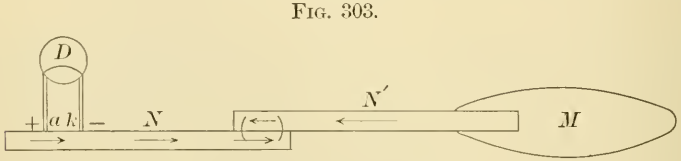
If the tube be filled with zinc sulphate solution, the galvanometer gives no evidence of electrotonic currents; but if a number of little glass beads be run along the axis, the spaces between the beads corresponding to the nodes of Ranvier in the nerve, the galvanometer will be at once

deflected, the conductor having been converted from a homogeneous into a heterogeneous one. The different facts just referred to, established by Funke, Gruenhegen, Hermann, etc., all go to show that the living nerve is a heterogeneous conductor, consisting (Fig. 302) of a central axis, which is a better conductor than its surrounding envelopes, the white subtance of Schwann, and the neurilemma, and that, owing to the inner polarization set up between the axis and its sheath, a resistance is offered to the polarizing current, hence its escape in longitudinal loops, the extent of which is proportional to the degree of polarization.

Secondary Electrotonus.

Just as a constant polarizing current traversing a nerve gives rise to an electrotonic current, so the latter gives rise to a secondary electrotonic current when made to traverse a second nerve. Thus, for example, if an excised nerve N (Fig. 303) be placed in contact with the nerve N' of a nerve-muscle preparation, and the former be stimulated the electrotonic current then developed in N will produce in

Fig. 303.



Secondary electrotonic current.

the nerve N' with which it is in contact a secondary electrotonic current which in stimulating N' causes the muscle to contract. That the contraction of the muscle is not due to a variation in the current of rest or to a current of action acting as stimuli, as might be supposed, but to the secondary electrotonic current, is shown by the fact that stimulation of the nerve by any other than electrical means will not cause contraction.

Electrotonic Modification of Excitability and Conductivity.

If a nerve when traversed by a constant polarizing current be still further tested as regards its excitability and conductivity, it will be found that the anodal and kathodal regions of the nerve differ not only as regards their electric potential, but also in the excitability and conductivity of the nerve being diminished in the anodal, and increased in the kathodal parts, that is of exhibiting the conditions known as anelectrotonus and katelectrotonus.[1]

The anelectrotonic and katelectrotonic conditions are not only interesting from being intimately connected in so many respects with the anelectrotonic and katelectrotonic currents, the latter, indeed, being so named for this reason by Du Bois Reymond, the phenom-

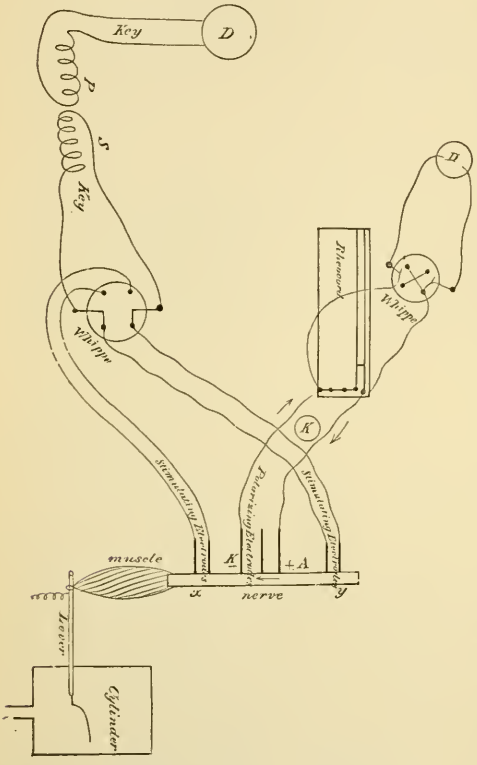
[1] Pflüger, Untersuchungen über die Physiologie des Electrotonus, 1859.

ena of anelectrotonus and katelectrotonus having been discovered first, but also on account of such conditions offering an explanation of certain well-established facts as regards the excitability of nerves by electrical stimuli. It might naturally be supposed in using the constant current as a nervous stimulant that the current would excite the nerve during the whole time that it was applied, that so long as the current passed through the nerve successive impulses would be generated, with the effect of throwing the muscle into a kind of tetanus. While under certain circumstances the above does take place, in the great majority of cases, however, the muscle remains entirely quiet during the passage of the current through the nerve, provided the current remains constant, contractions taking place at the making, or at the breaking, or at both the making and breaking, according as we shall see presently, to the strength and direction of the current. It may be said, therefore, as a general rule, that, during the passage of a constant current the muscle remains at rest. Nevertheless, as we have just seen, in the absence of any muscular contraction, the nerve is profoundly modified during the passage of a constant current by the development at the anode of the anelectrotonic current and anelectrotonic condition and at the kathode of the katelectrotonic current and katelectrotonic condition, conditions intimately connected with the peculiarities just referred to as regards the muscular contraction brought about by the opening and closing of the electrical circuit.

Before considering, however, these relations, let us first describe how the difference already mentioned in the excitability of the nerve at the anode and kathode, respectively, can be demonstrated. With this object, we will dispose the necessary apparatus, as represented in Fig. 304, and let us suppose, first, that the polarizing current thrown into the nerve by the opening of the key, and whose strength is regulated by the rheocord, is direct, descending—that is, traverses the nerve in the same direction as that of the nerve force—A being, therefore, the anode, and K the kathode. It will then be found that if the nerve be stimulated at the point x the irritability of the nerve will be increased during the passage of the polarizing current as shown by the greater elevation of the lever due to the muscular contraction, as compared with the average elevation previously determined with the same stimulus, but in the absence of the polarizing current. On the other hand, if the nerve be stimulated at the point y the irritability of the nerve will be found to be diminished. That it is not the distance of the point y from the muscle, as compared with that of x, to which the diminution in irritability at y is due, is shown by reversing the polarizing current by means of the whippe (its cross piece being in), so that the current becomes an inverse ascending one, the anode being then, therefore, nearer the muscle than the kathode; even then the irritability of the nerve at x is diminished, and, with certain qualifications, to be mentioned presently, that at y is increased. In this way, then,

it is shown that during the passage of a constant current the irritability of the nerve at the kathode is increased and at the anode diminished, the change in the condition of the nerve being described as that of katelectrotonus and anelectrotonus, or as the katelectrotonic increase, and anelectrotonic decrease of irritability. The condition of katelectrotonus and anelectrotonus not only modifies the irritability of the nerve as regards the originating of nervous impulses, but appears also to influence their propagation—at least it may be said that the condition of anelectrotonus offers an obstacle to the passage of a nervous impulse. The condition of katelectrotonus and anelectrotonus not only spreads out along the extrapolar portions of the nerve, but extends also into the intrapolar portion, the point where they merge into each other—that is, where the irritability is unchanged—being known as the neutral or indifferent point. The position of the latter varies somewhat, according to the strength of the current, with a strong current approaching the kathode, with a weak one the anode. While the katelectrotonic increase and anelectrotonic decrease of irritability reach a maximum shortly after the making of the polarizing current, and then gradually diminish, the katelectrotonic increase attains its maximum and minimum limits sooner than the anelectrotonic decrease. The strength of the katelectrotonic and anelectrotonic conditions depends, up to a certain limit, upon the strength of the polarizing current, and the general irritability of the nerve. With the opening of the polarizing current the phenomena of katelectrotonus and anelectrotonus disappear, there is, however, momentarily an increase of irritability at the anode, a decrease at the kathode. In bringing about this condition of katelectrotonus and anelectrotonus, while usually the

FIG. 304.



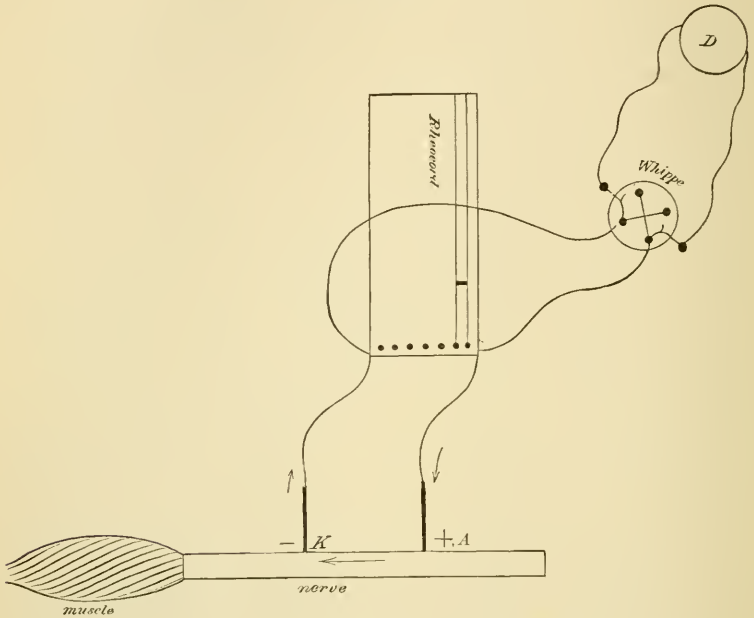
Disposal of apparatus to demonstrate electrotonic modification of excitability of nerve.

constant current is made use of as the stimulus, as in the preceding instance, this is not indispensable, an induced current producing the same effect; this is as might be expected, since a single induction shock may be regarded as a constant current, but of very short duration, developing very suddenly, and disappearing more gradually. Whether, therefore, the constant or induced current be used as a stimulus the nerve is thrown into the condition of katelectrotonus and anelectrotonus, and with the disappearance of the current, as just mentioned, there is a rebound at the poles, their condition being then momentarily reversed. It will be also particularly observed that during the passage of the current through the nerve the muscle remains quiescent, contraction only taking place if the strength of the current varies, or at the entrance or exit of the current into or from the nerve. The stimulus causing the nervous impulse is due to a change from one condition to another, not to the condition itself, the effect not depending so much upon the intensity of the condition as on variation of the same. Indeed, if the nerve be stimulated with a current the strength of which is very gradually increased or decreased the excitement generated will not suffice to cause muscular contraction. Further, it will be observed by extending the experiments, that a nervous impulse is only generated when the nerve passes from its normal condition into that of katelectrotonus, or that of increased irritability, and diminished electrical potential, or passes from the condition of anelectrotonus, that of diminished irritability and increased electrical potential, back to the normal condition, the latter normal condition being then, relatively at least, one of katelectrotonus, as compared with the immediately preceding anelectrotonic condition. As might be expected, however, the passage of the nerve from the anelectrotonic to the normal condition is far less effective as a generator of nervous impulses than that from the normal to the katelectrotonic condition, since the return from the anelectrotonic to the normal condition is a gradual, not a sudden one, and the change acts as a stimulus, at best only relatively. Hence, with constant currents at least, the muscular contraction takes place usually only at the closing, not at the opening of the current.

Let us now modify the arrangement of the apparatus just used so that (Fig. 305) by means of the rheocord we can modify the strength of the constant current, and, by the whippe (its cross piece being in), reverse with the cross in the direction through which it traverses the nerve, and let us suppose first that the current is a weak one, descending direct at the moment of stimulation—that is, at the making of the circuit, the muscle will contract, remaining quiet, however, during the passage of the current and also at the breaking of the same. Let us now reverse the direction of the current, so that it becomes an inverse ascending one (Fig. 306), then, as before, the muscle will contract only at the making of the circuit. The effect in both instances being the same, can be accounted for by

supposing the katelectrotonic condition acts as a stimulus, the impulse generated at the kathode in the case of the inverse current being still effective, even though the distance of the kathode from the

Fig. 305.

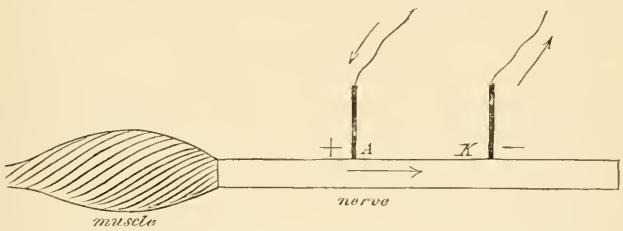


Disposal of apparatus to demonstrate effect of direct current upon excitability of nerve.

muscle is increased. Since, however, the latter impulse generated at the kathode has to traverse the anelectrotonic portion of the nerve (*a*), which, as it will be remembered, offers an obstacle to the propagation of the impulse, the muscular contraction due to the making of the inverse current will be less than that due to the making of the direct one. That no contraction takes place at the breaking of the circuit with either the direct or inverse currents is to be expected, since, with the breaking of the direct current, the kathode offers an obstacle, having become momentarily the anode, to the propagation of the impulse due to the weak katelectrotonic condition momentarily developed at the anode, and, with the breaking of the inverse current, the fall at the anode from anelectrotonus to the normal is too slight to generate an impulse. Let us now intensify the current and reverse its direction by the whippe, so that it is again a direct one (Fig. 305): muscular contraction will take place both at the making and breaking of the circuit, in the latter case the effect being due to the passage of the anelectrotonic condition back to the normal—that is, relatively to a condition of katelectrotonus. Reverse the current so as to make it an ascending one (Fig. 306), and, as before, we will have muscular contraction taking place both at the making and

breaking of the circuit; the katelectrotonic condition generating the impulse at the making and the return of the anelectrotonic condition to the normal at the breaking of the circuit. Finally, with a very strong current, if the latter be direct (Fig. 305), contraction takes place only at the making of the circuit, and with the inverse

FIG. 306.



Disposal of apparatus to demonstrate effect of inverse current upon excitability of nerve.

current only at the breaking. The fact of there being no contraction at the breaking of the circuit with the direct current may be accounted for, by partly supposing that the general irritability and conductivity of the intrapolar portion of the nerve has been depressed by the strong current, and partly by the fall of anelectrotonus not being effective, on account of the relative anelectrotonic condition, developed through the fall of the katelectrotonic condition, offering an obstacle to the transmission of the impulse. On the other hand, with the ascending current (Fig. 306) there will be no contraction at the making of the circuit, since the anelectrotonic condition, an obstacle to the propagation of the impulse generated at the kathode, intervenes between the latter and the muscle; but, with the breaking of the circuit, the fall of the anelectrotonus to the normal relatively katelectrotonus will generate an impulse, since no obstacle intervenes then between the point of stimulation and the muscle, and the latter will contract. The above facts, established among others by Pfaff, Ritter, and Pflüger, may be summarized as a law of muscular contraction, under the following formula, in which the direct and inverse currents are indicated by the letters *D* and *I* and the arrows, and the making and breaking of the circuits by the letters *M* and *B*, and the contraction and rest of the muscle by *C* and *R* respectively.

LAW OF MUSCULAR CONTRACTION.

	Weak current.	Medium current.	Strong current.
D ↓	*M C, B R,*	*M C, B C,*	*M C, B R,*
I ↑	*M C, B R,*	*M C, B C,*	*M R, B C,*

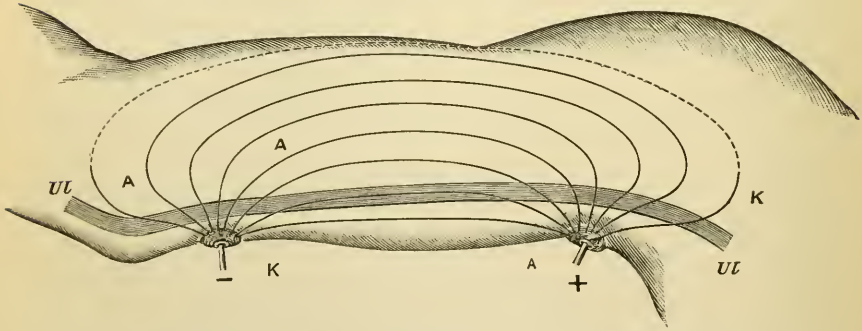
The above law can be readily remembered, and the facts explained, if it be admitted that muscular contraction only takes place when there is a rise of katelectrotonus or a fall of anelectro-

tonus (relative katelectrotonus); but not by the rise of anelectrotonus or fall of katelectrotonus (relative anelectrotonus). Or, in other words, that the nerve impulse starts at the kathode with the closing current and at the anode with the opening one. It may be mentioned in this connection that the closing and opening of a constant current traversing a nerve is frequently followed by a series of muscular contractions, respectively known as the closing tetanus of Wundt and the opening tetanus of Rutter.

Electrotonus in Man.

Inasmuch as the statements just made as to the modification of the excitability of a nerve by the passage of a constant current are based entirely upon experiments made on the isolated nerve of the frog, it is not to be expected that the results obtained by stimulating a human nerve covered by tissue and skin with a constant current will be exactly the same. Notwithstanding however the difference of the conditions in the two cases, it has been shown[1] that superficially lying motor nerves in man are thrown into a condition of electrotonus by the application of a constant current. It should be mentioned, however, that when the electrodes of the polarizing current are applied to the surface of the body as the current density diminishes in proportion to the distance of the underlying nerve from the surface, the intervening tissues being good conductors, the current soon leaves the nerve, in consequence of which the kathode comes to lie near the anode. It is for this reason that the electrodes of the polarizing and stimulating currents should be conjoined in one circuit so that the same tract of nerve can be stimulated simul-

Fig. 307.



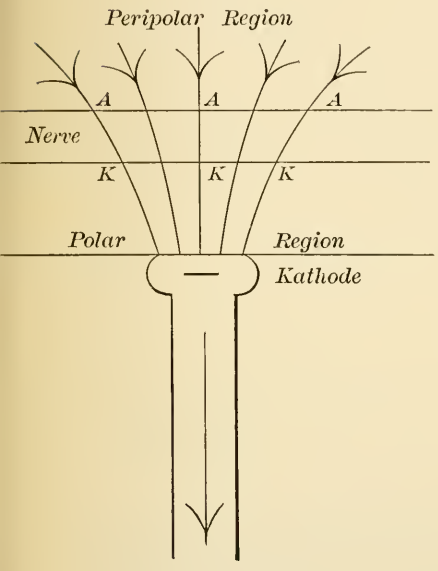
Scheme of the distribution of an electrical current in the nerve on galvanizing the ulnar nerve. (Landois.)

taneously or consecutively.[2] In considering the influence exerted upon the excitability of a nerve by the transmission of a constant current, one electrode should be applied first, the circuit being closed

[1] Eulenberg, Deutsches Archiv für klin. Medecin, Band iii., 1867, s. 117; Erb, Ebenda, s. 238, 513. [2] Waller, Phil. Trans., 1882, p. 961.

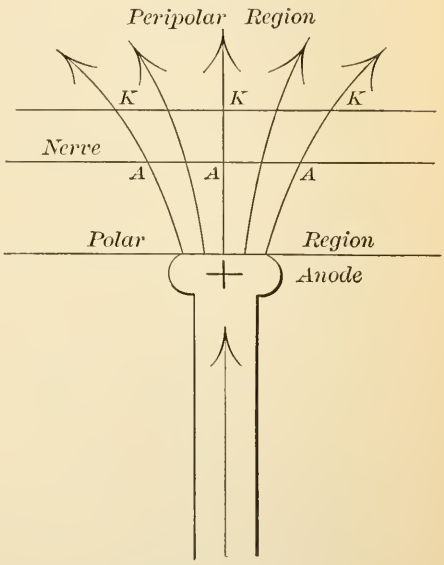
by the application of the other electrode to any convenient part of the body and the effect studied, and then the second electrode should be applied, the circuit being closed by the first one. Let us suppose that the anode is applied first to the surface, for example, of the arm overlying the ulnar nerve (Fig. 307 +), it will be observed that the points under the physical anode *A* in the polar region, where the current enters the nerve constitute a group of physiological anodes (Fig. 309, *A A A*), and where the current leaves the

Fig. 308.



Exit of current from arm.

Fig. 309.



Entrance of current into arm.

nerve, in the peripolar region, a group of physiological kathodes *K K K*, and that the points under the physical kathode *K*, where the current enters the nerve in the peripolar region, constitute a second group of physiological anodes (Fig. 308) *A A A*, and where the current leaves the nerve in the polar region, a second group of physiological kathodes *K K K*.

It is obvious, therefore, that there are four possible cases which can be tabulated, the muscular contraction being taken as the measure of the excitability of the nerve, as follows :

1st. Kathodic closing contraction *KCC*, *i. e.*, the effect of the change developed at the physiological kathode beneath the physical kathode. 2d. Anodal closing contraction *ACC*, *i. e.*, the effect of the change developed at the physiological kathode beneath the physical anode. 3d. Anodal opening contraction *AOC*, *i. e.*, the effect of the change developed at the physiological anode beneath the physical anode. 4th. Kathodal opening contraction *KOC*,

i. e., the effect of the change developed at the physiological anode beneath the physical kathode. These four contractions differ very much, however, in strength, owing to the fact that with a closing current the excitement starts at the kathode, but with an opening current at the anode, that the excitement developed at the kathode on closing the current is stronger than that developed at the anode on opening it, and that the effect of the current is proportional to its density. Thus, for example, of the four contractions the two closing ones *KCC* and *ACC* are stronger than the two opening ones *AOC* and *KOC* since the excitement developed at the physiological kathode with a closing current other things equal is stronger than that developed at the physiological anode with an opening one. Of the two closing contractions the *KCC* is, however, stronger than the *ACC* since the current in the polar region at the physiological kathode beneath the physical kathode is denser[1] than in the peripolar region at the physiological kathode beneath the physical anode. On the other hand of the opening contractions *AOC* is stronger than *KOC* because the current in the polar region at the physiological anode beneath the physical anode is denser than in the peripolar region at the physiological anode beneath the physical kathode.

The above conditions may be briefly tabulated as follows:[2]

Current.	Stimulus.	Region.	Condition.
KCC.	Kathodic.	Polar.	Best stimulus in best region.
ACC.	Kathodic.	Peripolar.	" " worst region.
AOC.	Anodic.	Polar.	Worst stimulus in best region.
KOC.	Anodic.	Peripolar.	" " worst region.

Finally, if instead of comparing the contractions obtained with a current of constant strength the order in which they appear be observed with currents of gradually increasing strength, it will be found that the KCC appears first, the KOC last, the formula for contraction being, in man, as follows:

Weak current, KCC.
Medium " KCC.—ACC.—AOC.
Strong " KCC.—ACC.—AOC.—KOC.

In concluding our account of general nerve physiology it remains for us now to say a few words with reference to the conditions influencing the general irritability of nerves, which for convenience' sake have been reserved for the present moment, such as the influence exerted by the distance from the muscle of the point of the nerve stimulated, the effect of the angle at which the current enters and leaves the nerve, the duration and number of the stimuli, the temperature and blood supply, the functional activity,

[1] As the same amount of electricity always flows through any given transverse section of the circuit, the density of the current will be greater in a thin conductor than in a thick one.

[2] Waller, Human Physiology, 1891, p. 363.

severance from the central nervous system, etc. Thus, if two pairs of electrodes are placed upon the nerve of a freshly prepared nerve-muscle preparation, one pair near the muscle, the other pair near the cut end of the nerve, it will be found that the muscular contraction is greater when the stimulus is applied through the latter pair than when through the former. This result can be accounted for either on the supposition that the nervous impulse gathers strength, avalanche-like, as it travels from the cut end of the nerve toward the muscle, or that the central end of the nerve is more irritable than the distal end. The latter view is the most probable, since the current of action, or negative variation, exhibits no such avalanche-like increase as it progresses, wave-like, from the point stimulated to the muscle. In stimulating a nerve it is important that the electrode should be so applied that the current will pass through the nerve as nearly longitudinally as possible, not transversely, as in the latter case the current will not produce any effect.[1]

It has been shown by Konig[2] that the constant current if used as a stimulus must last at least the 0.0015 second to produce a nervous impulse, and by Kroniker and Stirling,[3] that inductive shocks even if repeated as rapidly as 2200 times a second will throw a muscle into tetanus. In this connection it may be mentioned that according to Helmholtz,[4] that if maximum induction shocks be thrown into a nerve following each other at a rate of less than the $\frac{1}{600}$ of a second, half the shocks will produce no effect, the muscle being devoid of irritability for the $\frac{1}{600}$ of a second subsequent to each shock.

The influence exerted by the duration and change of intensity of the stimulus upon excitability differs in nerves as compared with striated and unstriated muscles. Thus, for example, in the case of nerves, rapid change of intensity is more important than duration of stimulus, in striated muscles the reverse obtains while in unstriated muscles duration of the stimulus is the all important factor.[5] A rise of temperature, say to 45° C. (113° F.) in the case of the frog's nerve favors the development of nerve irritability, the activity of the molecular processes being increased, nervous impulses are generated more readily by stimuli, and the muscular contractions are proportionately greater. On the other hand, the application of cold benumbs the nervous system, diminishes nervous irritability, the latter disappearing altogether if the temperature be reduced to 0° C. (32° F.). Judging from what we shall learn hereafter from the analogous case of muscle there can be little doubt that the irritability of a nerve depends upon a full supply of oxygenated blood and that through prolonged use the nerve becomes exhausted. Finally, if a nerve be divided in the

[1] Albrecht v. Meyer, Pflüger's Archiv, Band xxi., 1880, s. 462.
[2] Wien. Sitz. Bericht, lxii., 1870.
[3] Archiv Anat. u. Phys., 1878, s. 1.
[4] Berlin Monats. Bericht, 1854.
[5] Fick, Beiträge zur Physiologie der irritabilen Substanzen, 1863.

living body or even out of it, it will be observed that at the peripheral end of the cut nerve the irritability at first slightly increases, then diminishes, and finally disappears, the changes in the irritability advancing from the cut end of the nerve toward the muscle. (Ritter-Valli law.) Coincidently with the changes in the irritability of the nerve just mentioned, a degeneration is set up in the substance of Schwann and the axis-cylinder extending to the terminal filaments, involving even their endings in the motor plates. A similar degeneration may extend also centripetally from the cut end, but not beyond the first node of Ranvier. Beyond this point the nerve is usually found normal.

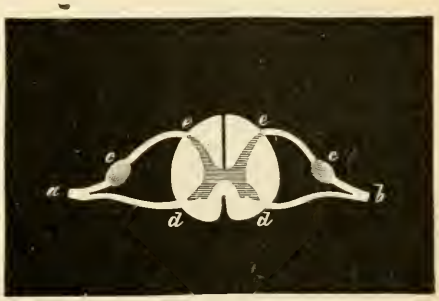
CHAPTER XXX.

THE NERVOUS SYSTEM.—(*Continued.*)

THE SPINAL CORD, ITS STRUCTURE AND FUNCTIONS AS A CONDUCTOR OF EFFERENT AND AFFERENT IMPULSES.

The spinal cord lying in the vertebral canal, enveloped within its membranes, extends as a cylindrical cord of from 37 to 45 cm. (15 to 18 inches) in length from the medulla oblongata, with which it is continuous, at the level of the occipital foramen to the lower part of the first lumbar vertebra. It weighs about 28 grammes (1 ounce). If a transverse section of the cord be made, it will be observed (Fig. 310) that it consists of white matter externally, and of gray matter internally, the latter being found in the greatest amount opposite the cervical and lumbar enlargements, the origin of the large nerves. The gray matter is disposed as two crescents, placed back to back, somewhat in the form of the letter H and connected across the middle line by an isthmus, the gray commissure, each crescent exhibiting an anterior, a posterior cornu or horn, and a middle part, the cervix or neck.

Fig. 310.

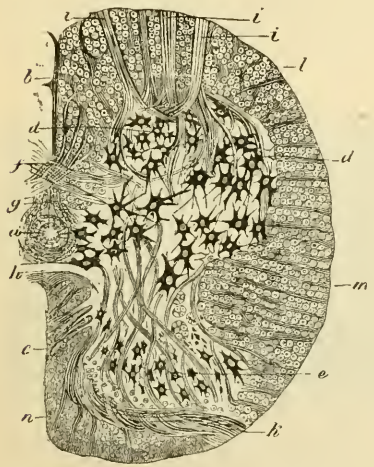


Transverse section of the spinal cord. *a*, *b*. Spinal nerves of right and left sides. *d*. Origin of anterior root. *e*. Origin of posterior root. *c*. Ganglion of posterior root. (Dalton.)

The gray commissure is often subdivided into the interior and posterior gray commissures by its central canal, which, as we shall see hereafter, is the remnant of the primitive neural canal. This peculiar arrangement of the gray matter within the spinal cord serves conveniently to subdivide the white portions of the cord into the anterior, lateral, and posterior columns. The anterior columns are made up by that part of the white matter of the cord lying between the anterior median fissure and the anterior cornu. It will be observed, however, that, as the anterior median fissure does not extend into the anterior gray commissure, a band of white matter, the white commissure, intervening, the anterior columns run into each other, and that, as the anterior cornu does not extend to the outer edge of the cord, the anterior columns pass into the lateral

ones, lying between the two crescents. On the other hand the posterior median fissure filled up with the inner layer of the pia mater and extending down to the posterior gray commissure, and the posterior cornu of the gray matter to the inner edge of the cord, the posterior columns lying between them are completely separated from the lateral columns, and from each other. In certain regions of the cord each posterior column is further subdivided by a rather obscure fissure into two sub-columns, the one, the posterior median column, lying immediately next to the posterior median fissure, often called the column of Goll, also the inner root zone of Charcot, the other the posterior external column, or the column of Burdach, or the outer root zone of Charcot, the two columns terminating respectively in the clavate and the cuneate nuclei of the medulla. The white matter of the cord constituting its columns as just described consists principally of medullated nerve fibers which, though provided with neurokeratin sheaths, do not possess a neurilemma.

Fig. 311.



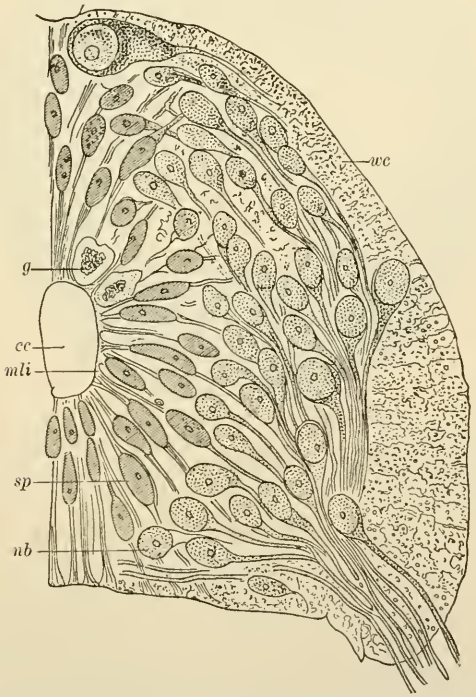
Transverse section through the under half of the human cord. *a*. Central canal. *b*. Anterior, *c*, Posterior fissure. *d*, Anterior cornu, with large ganglion cells. *e*. Posterior cornu with smaller. *f*. Anterior white commissure. *g*. Sustentacular substance around the central canal. *h*. Posterior gray commissure. *i*. Bundles of the anterior, and *k* of the posterior spinal nerve roots. *l*. Anterior, *m*, Lateral, *n*, Posterior column. (Deiters.)

The course of the fibers through the columns of the cord is generally in a longitudinal direction, those decussating in the white commissure and in the gray matter as well as the fibers entering into the formation of the roots of the spinal nerves are, however, transversely or obliquely disposed. If the white matter of the cord be viewed in transverse sections with the microscope, the nerve fibers will then appear like small circles of different sizes (Fig. 311), with a rounded dot in the center, the latter, or the axis-cylinder, being very distinct if the preparation be stained with carmine, while between groups of these nerve fibers fine septa of connective tissue may also be observed supporting delicate blood vessels. The gray matter of the cord consists of a supporting connective tissue, the neuroglia of Virchow, composed of a fine network of round and large branched cells, imbedded in a homogeneous matrix, which, from being particularly abundant at the sides of the posterior cornu, is there known as the gelatinous substance of Rolando, of blood vessels derived from the vertebræ and partly from the intercostal lumbar and sacral arteries of nerve cells and nerve fibers.

The cells in the gray matter of the cord are of two kinds, large multipolar cells (Fig. 311, *d*), such as are found in the anterior cornu, and small spindle-shaped cells (*e*) in the posterior cornu. Large multipolar cells are also found principally in the lower part of the dorsal region of the cord, behind the gray commissure, and on the inner surface of the posterior cornu, constituting the posterior vesicular column of Clarke.

The gray matter of the cord consists also, or is traversed, rather, by innumerable delicate non-medullated nerve fibers, which appear to be the axons or the outgrowths of the cells just mentioned, and which pass either into the roots of the spinal nerves or into the columns. On account, however, of the manner in which the sections are made necessarily, in many cases it is impossible to say anything positively as to either the origin or termination of such

FIG. 312.

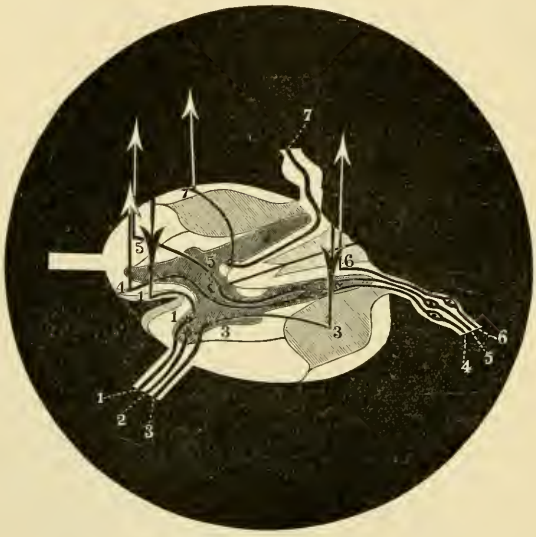


Transverse section of half of the spinal cord of a trout embryo. *cc.* Central canal. *mli.* Membrana limitans interna. *g.* Germinal cell. *sp.* Spongioblast. *nb.* Neuroblast. *wc.* White columns, (LANDOIS.)

nerve fibers. Comparison of sections made, however, both in a longitudinal and in a transverse direction, leads to the supposition that all such non-medullated nerve fibers, or axis-cylinders, found in the gray matter of the cord, originate in either encephalic or spinal cells, neuroblasts (Fig. 312), and, directly or indirectly,

through spinal nerves, terminate in muscle, gland, sensory organ, etc. What has been positively learned from the recent histological researches of Lenhossek,[1] Obersteiner,[2] Koelliker,[3] and others as to the origin and course of these fibers may be briefly summed up as follows: The axis-cylinders of the anterior roots terminating in the muscle end-plates[4] pass out of the cord continuously as the axons, of the cells, of the anterior cornu, the latter being situated near the end tufts of the axons, of the cerebral cells. Of the latter axons some (Fig. 313), pass through the white commissure, and are continued

Fig. 313.



Course of the motor and sensory paths in a spinal segment. 1. Anterior pyramidal tract. 3 Crossed pyramidal tract. 4 and 5. Sensory paths decussating in the cord. 6. Sensory paths which do not decussate in the cord. 7. Afferent paths leading to Clarke's column and from thence passing as uncrossed fibers upwards *viâ* the direct cerebellar tract. 2. Origin of a motor fiber from a ganglionic cell of the anterior cornu. (Landois.)

as the direct pyramidal tract in the anterior column of the opposite side of the cord, while others 3 (Fig. 313), pass into the lateral columns of the same side, and thence to the medulla oblongata, where the greater portion, decussating with the corresponding fibers of the opposite side, pass as the crossed pyramidal tract through the pons, crusta of the crus cerebri, to the caudate and lenticular nuclei of the corpus striatum and by the anterior two-thirds of the posterior segment of the internal capsule to the motor areas of the cerebral cortex (Fig. 314). The axis-cylinders of the posterior roots,[5] after enter-

[1] Der Feinere Bau des Nervensystems, etc., Zweite Auflage, 1895, s. 248.
[2] Anleitung Beim Studium des Baus der Nervösen, Centralorgane, etc. Dritte Auflage, 1896, s. 208.
[3] Handbuch der Gewebelehre des Menschen, Sechste Auflage, Zweiter Band, 1896, s. 55. [4] See Fig. 241, p. 484. [5] See Fig. 242, p. 484.

ing the spinal cord, divide into ascending and descending branches, the end tufts of which lie in close proximity to cells whose axons cross the middle line of the cord and ascend by the anterior and lateral columns of the opposite side (Fig. 313, 4, 5)

FIG. 314.

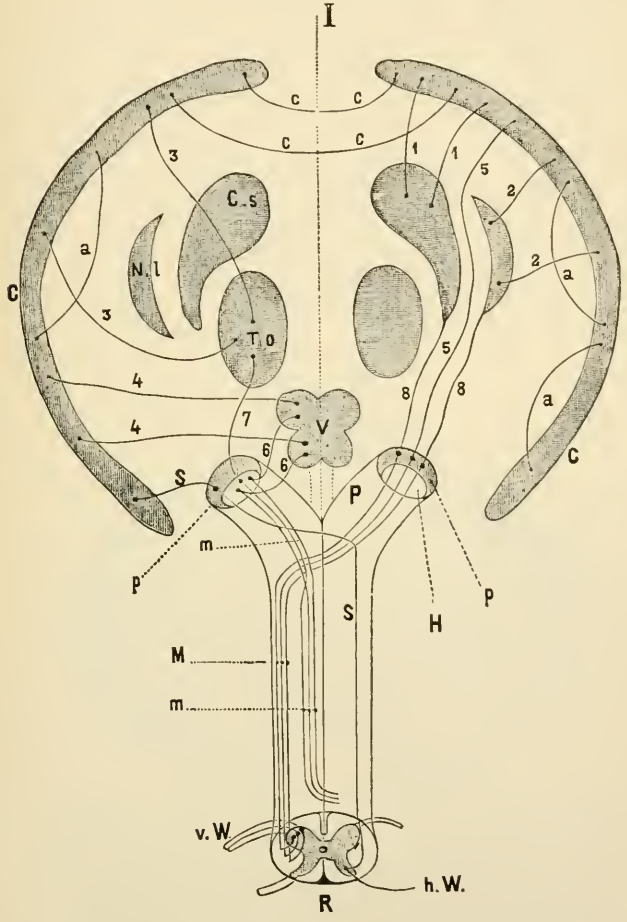


Diagram of the structure of the brain. C C. Cortical substance of the cerebral hemispheres. C. s. Corpus striatum. N. l. Nucleus lenticularis. T. o. Thalamus opticus. V. Corpora quadrigemina. P. Pedunculus cerebri. P. Basis or crusta, and H, tegmentum. 1, 1. Fibers of the corona radiata of the corpus striatum. 2, 2. Those of the lenticular nucleus. 3. Those of the optic thalamus. 4, 4. Those of the corpora quadrigemina. 5, 5. Direct strands to the cortex cerebri (Flechsig). 6. Fibers from the corpora quadrigemina to the tegmentum. 7. Fibers from the optic thalamus to the tegmentum. m. Further course of these fibers. 8. Fibers from the corpus striatum and lenticular nucleus to the pes of the pedunculus cerebri. M. Further course of these fibers. S, S. Course of the sensory fibers. R. Transverse section of the spinal cord. v W. Anterior roots. h W. Posterior roots of the spinal nerves. a, a. Association fibers. c, c. Commissural fibers.

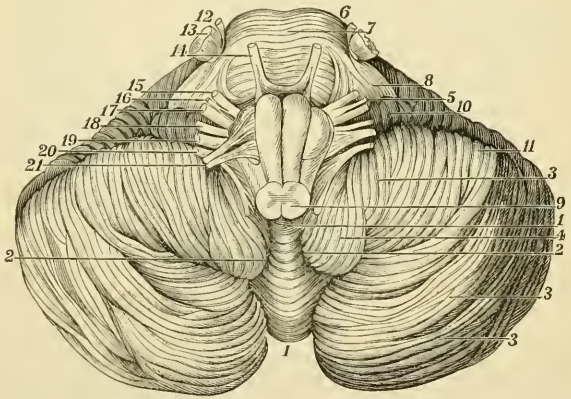
through the medulla, pons, and tegmentum of the crus to the thalamus opticus and to the posterior third of the posterior segment of the internal capsule or the "sensory cross-way" to the sensory areas of the cerebral cortex. The fibers just described, connecting

the cerebral cortex and the anterior and posterior roots, we shall see presently, constitute the avenues by which motor impulses pass from the brain to the periphery, and sensory ones from the periphery to the brain. The anterior and posterior roots consist, as incidentally mentioned, not only of motor and sensory fibers but of other fibers as well, which take a different course through the cord and have different functions, the consideration of which will be deferred, however, for the present.

From what has just been said, it is obvious that, while for convenience' sake, the spinal cord may be described as beginning at the great foramen, as a matter of fact, it passes so continuously into the medulla that the latter may be regarded as its upper expanded portion, and, since the medulla is largely made up of fibers passing through it to and from the cortex, corpora striata, thalami optici, etc., the cord, physiologically, may be regarded as beginning in these basal ganglia and the cortex rather than at the great foramen.

The medulla oblongata (Fig. 315) is of a pyramidal form, hav-

Fig. 315.



Inferior surface of the cerebellum with the pons Varolii and medulla oblongata. 1. Placed in the notch between the cerebellar hemispheres, is below the inferior vermiform process. 2, 2. Median depression, or vallecula. 3, 3, 3. The biventral, slender, and posterior inferior lobules of the hemisphere. 4. The amygdala. 5. Flocculus, or subpeduncular lobule. 6. Pons Varolii. 7. Its median groove. 8. Middle peduncle of the cerebellum. 9. Medulla oblongata. 10, 11. Anterior part of the great horizontal fissure. 12, 13. Smaller and greater roots of the fifth pair of nerves. 14. Sixth pair. 15. Facial nerve. 16. Pars intermedia. 17. Auditory nerve. 18. Glosso-pharyngeal. 19. Pneumogastric. 20. Spinal accessory. 21. Hypoglossal nerve. (From Sappey, after Hirschfeld and Leveillé.)

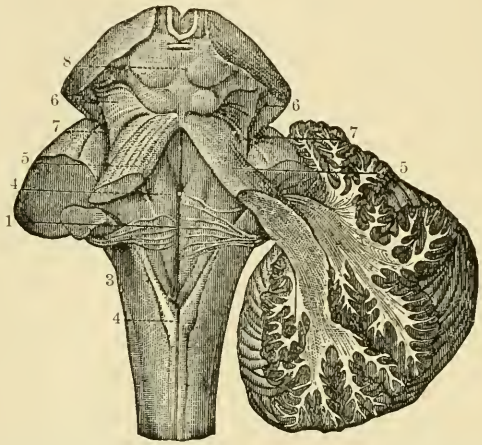
ing its broad extremity upward and expanded laterally at its upper part. Its length is about an inch and a quarter, its breath nearly an inch, and its thickness about three-quarters of an inch. Like the spinal cord, the medulla presents two median fissures. The anterior median fissure terminates just below the pons in a recess, the foramen cæcum of Vicq d'Azyr; the posterior median fissure is, however, continued up into the floor of the fourth ventricle, where, after expanding into a superficial furrow, it is gradually lost. In other respects, however, the medulla differs entirely in the arrangement of

its parts from the spinal cord, each of its halves being characterized by four eminences, or columns, which are known in the order in which they present themselves from before backward as the anterior pyramids, the olivary bodies, the restiform bodies, and the posterior pyramids. The anterior pyramids are situated on either side of the anterior fissure, and are separated from the olivary bodies by a slight depression. Each anterior pyramid consists of two sets of fibers, inner and outer: the outer fibers are continuations of those of the anterior columns of the cords of the same side, and, together with the decussating fibers from the opposite side of the cord, pass upward through the pons into the cerebral peduncles; the inner or decussating fibers, so called because they interlace, to a considerable extent, with those of the opposite pyramid, are, in reality, almost entirely derived from the fibers of the lateral column of the opposite side of the cord, the anterior pyramids being pushed aside, as it were, by the lateral columns inserting themselves between them as they interlace with each other. The anterior pyramid proper contains no gray matter, its so-called nucleus consisting of stellate nerve cells lying behind and between it and the olivary body. The olivary bodies are two smooth, oval eminences sunk deeply into the medulla, and consist of both white and gray matter; the fibers of the former run in a longitudinal direction. The gray matter, presenting a very characteristic zigzag contour in section, is known as the corpus dentatum, or ciliare, or olivary nucleus; while the gray lamina above the latter is often described as the accessory olivary nucleus. The fibers of the anterior columns of the cord, which, as just mentioned, are thrown outward as they are continued up as the outer fibers of the anterior pyramids, pass partly on the outside of, and partly beneath the olivary bodies, and being joined by fibers from the olivary nucleus pass upward as the olivary fasciculus and fillet to the corpora quadrigemina and cerebral peduncles. The restiform bodies, or the inferior peduncles of the cerebellum, situated behind and to the outer side of the olivary bodies (Fig. 316), while containing a considerable quantity of gray matter, consist principally of white fibers continued upward partly from the posterior column of the cord, and partly from the lateral and anterior columns; the latter fibers, a small band, connect the anterior column with the cerebellum. The posterior pyramids situated on either side of the posterior median fissure, containing much gray matter, consist of white fibers, continuous with those of the posterior median columns of the cord; ascending, they diverge from one another, forming the lower boundary of the fourth ventricle, and tapering off become closely applied to the restiform bodies.

Resuming what has just been said with reference to the structure of the medulla, it will be seen that the fibers of the anterior columns of the cord pass through it by three routes: 1st, as the fibers of the anterior pyramids to the cerebral peduncles; 2d, as the inner fibers of the anterior pyramids (together with the decussating fibers), as

the olivary fasciculus and fillet to the corpora quadrigemina and cerebral peduncles; 3d, as the band behind the olivary body, from the restiform body to the cerebellum. The fibers of the lateral columns pass through the medulla also by three routes: 1st, as the decussating fibers (together with the inner fibers of the anterior pyramids), as the olivary fasciculus and fillet to the corpora quad-

Fig. 316.



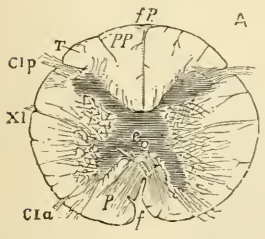
View of the floor of the fourth ventricle with the posterior surface of the medulla oblongata and neighboring parts. On the left side the three cerebellar peduncles have been cut short; on the right side the white substance of the cerebellum has been preserved in connection with the superior and inferior peduncles, while the middle one has been cut short. 1. Median groove of the fourth ventricle with the fasciculi teretes, one on each side. 2. The same groove at the place where the white striæ of the auditory nerve emerge from it to cross the floor of the ventricle. 3. Inferior peduncle or restiform body. 4. Posterior pyramid; above this the calamus scriptorius. 5. Superior peduncle, or processus a cerebello and cerebrum; on the right side the dissection shows the superior and inferior peduncles crossing each other as they pass into the white center of the cerebellum. 6. Fillet to the side of the crura cerebri. 7. Lateral grooves of the crura cerebri. 8. Corpora quadrigemina. (From Sappey after Hirschfeld and Leveillé.)

rigemina, and cerebral peduncles; 2d, by the restiform body to the cerebellum; 3d, by the fibers in the floor of the fourth ventricle (fasciculus teres) into the cerebrum. The fibers of the posterior columns pass through the medulla by two routes: 1st, the outer portions of the columns by the restiform bodies to the cerebellum; 2d, the inner portion (fasciculus gracilis), by the posterior pyramids to the cerebrum.

The fourth ventricle (Fig. 316), just alluded to incidentally, is the space left between the medulla oblongata in front, and the cerebellum behind. It is bounded laterally by the superior peduncles above, and by the diverging posterior pyramids and restiform bodies below, and is covered in behind by the valve of Vieussens and inferior vermiform process of the cerebellum, the floor being constituted by the back of the medulla oblongata and pons Varolii, marked by the median furrow terminating inferiorly as the calamus scriptorius; above the fourth ventricle communicates through the sylvian aqueduct or iter with the third ventricle,

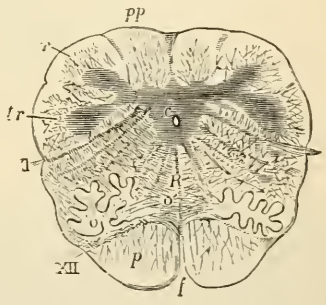
and below with the central canal of the spinal cord and the subarachnoid cavity through the foramen of Magendie in the pia mater. The gray matter of the floor of the fourth ventricle disposed as a continuous series of nuclei extending from beneath the corpora quadrigemina to a point corresponding to the decussation of the pyramids, is of extreme interest physiologically as constituting, as we shall see, the nuclei of origin of the so-called cranial nerves from the third to the twelfth inclusive. The gray matter of the medulla, like that of the spinal cord proper, differs as regards its form, amount, etc., according to the position of the section. Thus, if the latter be made just above the level of the first cervical nerve (Fig. 317), the central gray substance is encroached upon, pushed back by the decussating fibers from the lateral columns, which, in coursing inward, separate the anterior cornu from the rest of the gray substance, while if the section be made through the lowest part of the olivary bodies (Fig. 318), the gray matter will be seen to be

FIG. 317.



Transverse section of cord just above level of first cervical nerve.

FIG. 318.



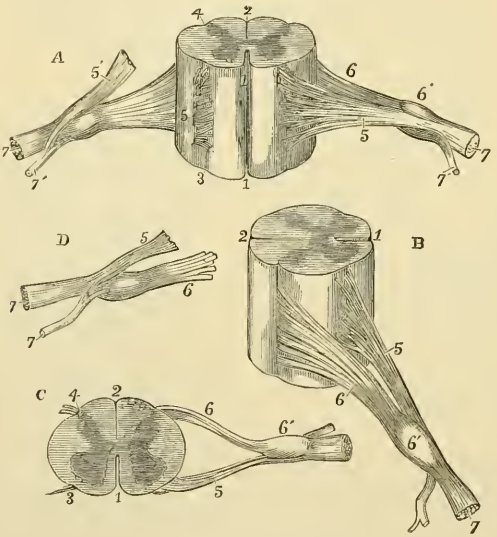
Transverse section of medulla at level of olivary bodies.

still further modified. The pons Varolii entering, as we have seen, into the formation of the floor of the fourth ventricle, consists not only of the longitudinal fibers passing upward through it from the cord and medulla to the crura cerebri, but also of commissural fibers connecting the lateral halves of the cerebellum and of gray matter. The functions of the latter will be considered after those of the spinal cord and medulla have been treated of.

From the fact of the spinal nerves being distributed in general to the muscles of the trunk and extremities, the sphincters, and to the integument covering these parts, of the posterior part of the head, and a portion of the mucous membrane, it is evident that a complete account of their functions would necessitate not only a detailed description of each spinal nerve, but of the parts supplied by the latter. Inasmuch, however, as the structure and functions of any one spinal nerve are essentially the same as those of the spinal nerves in general, a brief description of these nerves only will be given.

There are thirty-one pairs of spinal nerves, eight cervical, twelve dorsal, five lumbar, five sacral, and one coccygeal. Each spinal nerve (Fig. 319, A B) arises from the cord by an anterior and a posterior root, the latter being the largest, and having a ganglion. Immediately beyond the ganglion the two roots unite into a single spinal nerve, which, after passing out of the spinal canal by the intervertebral foramen (with the exception of the sacral and coccygeal nerves, which divide within it), divides into two branches, anterior and posterior, distributed respectively to the anterior and posterior portions of the body, the anterior branch being the larger. It will be observed that a distinction is made between the anterior and posterior roots and the anterior and posterior branches of a spinal nerve. This distinction is a most important one, it having been

FIG. 319.



Different views of a portion of the spinal cord from the cervical region, with the roots of the nerves slightly enlarged. In A, the anterior surface of the specimen is shown, the anterior nerve-root of its right side being divided; in B, a view of the right side is given; in C the upper surface is shown; in D the nerve-roots and ganglion are shown from below. 1. The anterior median fissure. 2. Posterior median fissure. 3. Anterior lateral depression, over which the anterior nerve-roots are seen to spread. 4. Posterior lateral groove, into which the posterior roots are seen to sink. 5. Anterior roots passing the ganglion. 5′. In A, the anterior root divided. 6. The posterior roots, the fibers of which pass into the ganglion 6′. 7. The united or compound nerve. 7′. The posterior primary branch, seen in A and D to be derived in part from the anterior and in part from the posterior root. (From QUAIN.)

well established that the anterior root is purely motor in function, and the posterior root purely sensory, whereas the anterior branch, consisting of fibers derived from both the anterior and posterior roots will be found to be both motor and sensory in function, and the posterior branch being made up also of fibers derived from both the anterior and posterior roots is also motor and sensory in function. The anterior and posterior branches of a spinal nerve are

therefore mixed in their function, whereas the anterior root is purely motor, and the posterior root wholly sensory.

The discovery that the anterior root of a spinal nerve is motor, the posterior root sensory in function, is an excellent illustration of the indispensability of vivisection as a means of research in physiological investigation—indeed, it is difficult to conceive how the discovery could have been made in any other manner, comparative anatomy, from the nature of the case, throwing no light upon the question, since the spinal nerves arise with the exception, perhaps, of Amphioxus in a similar manner in all vertebrates, while pathological changes, even when recorded from involving both roots simultaneously, rendered such data of little or no use. Such being the case, the only available means of investigation was experimental, and, as a matter of fact, it was by such means, a vivisection, that Magendie[1] first demonstrated the function of the roots of the spinal nerves, one of the most important discoveries ever made in the whole range of physiological science. The experimental procedure which can readily be repeated is as follows: The vertebral canal being laid open and the spinal cord and nerves exposed in a frog, for example, or a rabbit or dog, the anterior roots of the spinal nerves supplying the lower extremity are divided. Allowing sufficient time to elapse for the effect of shock, hemorrhage, etc., to pass off, it will be observed that the lower extremity on the same side as that on which the nerves have been divided is paralyzed so far as regards motion, sensation remaining intact. If, however, the distal end of the divided anterior roots (Fig. 320, *c*) be now stimulated, the lower extremity will be at once thrown into muscular contraction, whereas no effect is observed, on the other hand, of a motor character, if the central end *d* of the divided anterior root be stimulated. These facts show conclusively that the functions of the anterior roots of the spinal nerves are motor, and that the stimulus emanating from the cord, whatever its nature may be, is transmitted through the anterior root from the center to the periphery. That the anterior root possesses in itself no sensory properties, is shown from the fact, that even if at times signs of sensibility manifest themselves on its stimulation, such sensibility

Fig. 320.

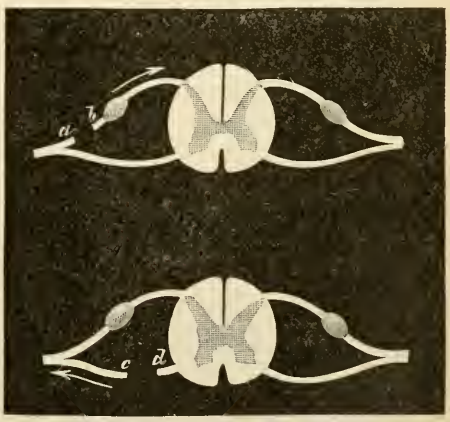
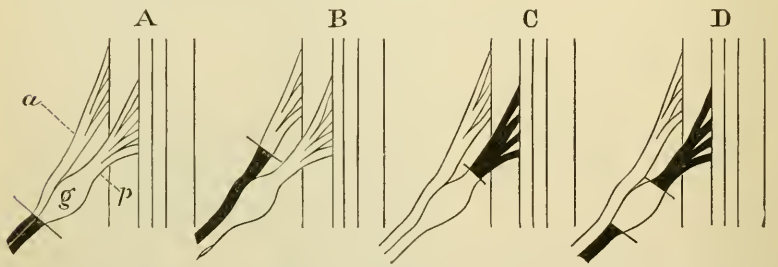


Diagram of spinal cord and nerves. The posterior root is seen divided at *a*, *b*, the anterior at *c*, *d*.

[1] Journal de Physiologie, Paris, 1822, Tome ii., pp. 276–368.

at once disappears after division of the posterior root. The sensibility occasionally exhibited on stimulation of the anterior root is due either to muscular cramp, as suggested by Brown-Séquard,[1] or to the recurring fibers passing backward from the anterior root through the posterior root to the cord, hence the name of "recurrent sensibility" given to the phenomenon by Magendie[2] and Longet.[3] If, now, the posterior roots of the spinal nerves in the same animal, but in an uninjured one, be divided, it will be observed that while the animal retains the power of moving the lower extremity it has lost sensation entirely in it, and that while no effect is observable if the distal end (*a*, Fig. 320) of the divided posterior root be stimulated, sensibility at once manifests itself if the central end (*b*) of the same be stimulated, showing conclusively that the function of the posterior root of the spinal nerve is sensory, and that the impression made upon the periphery is transmitted through the posterior root to the cord. That the posterior root possesses in itself no motor properties is shown from the fact that if the anterior root be divided no motion ever ensues on stimulating its central end (*b*, Fig. 320), any motion ensuing on stimulation of the central end of the posterior root being reflex in character, a kind of recurrent motility, so to speak—that is to say, the impression made upon the central end of the divided posterior root is transmitted to the gray matter of the cord, and is thence reflected out through the anterior root. While the ganglion already mentioned, so characteristic of the posterior roots of the spinal nerves, does not appear to influ-

Fig. 321.



Degeneration of spinal nerves and nerve roots after section. A. Section of nerve trunk beyond the ganglion. B. Section of anterior root. C. Section of posterior root. D. Excision of ganglion. *a*. Anterior root. *p*. Posterior root. *g*. Ganglion.

ence in any way the transmission of impressions from the periphery to the centers, it does exercise a very great influence upon the nutrition of the nerves after their division. Thus it has been shown by Waller,[4] if the anterior root be divided (B, Fig. 321), that while the central end of the anterior root preserves its normal structure,

[1] Physiology and Pathology of the Central Nervous System, p. 8. Philadelphia. 1860. [2] Comptes rendus, T. xxiv., p. 3. Paris, 1847,
[3] Bernard: Systeme Nerveux, Tome i., p. 35. Paris, 1858. Physiologie, Tome iii., p. 115. Paris, 1869.
[4] Comptes rendus, Tome xliv., p. 168. Paris, 1857.

the distal end degenerates, exhibiting the usual changes undergone by a nerve when separated from its center; whereas, in the case of the posterior root being divided between the ganglion and the cord (C, Fig. 321), it is the distal end, that attached to the ganglion, which remains normal, the central end degenerating. It would appear, therefore, from these experiments, that the ganglion of the posterior roots exerts a nutritive influence upon the sensitive nerves, like that exerted by the spinal or higher centers on motor ones, and it is worthy of observation that the degeneration takes place in the direction in which the nerve force is transmitted. In this connection it may be mentioned also, as confirmatory of the explanation offered of recurrent sensibility, that if the posterior root be divided beyond the ganglion the anterior roots will then be found to contain degenerated fibers, showing that some of the fibers of the anterior root at least are really derived from the posterior one.

It is generally held, though denied by some physiologists, that, while the gray matter of the cord transmits sensory impressions, it itself appears to be insensible to ordinary mechanical or electrical stimuli, since it may be pricked, pinched, or electrically stimulated without the animal giving any signs of pain. The gray matter can be, however, excited by chemical stimuli, certain poisons, and venous blood.

It has already been mentioned that the anterior and posterior roots of the spinal cord do not consist exclusively of purely motor and sensory fibers. Thus, for example, the vasomotor and sweat fibers regulating the calibre of the blood vessels and the production of sweat, leave the cord by the anterior root. The posterior roots contain also fibers which pass directly or indirectly to the anterior root, to the direct cerebellar tract (Fig. 313), and through the column of Burdach to the column of Goll, thence to the clavate nucleus of the medulla; other fibers, ascending the posterior columns, cross the middle line above the cuneate and clavated nuclei of the medulla and pass to the opposite hemisphere.

While there can be no doubt that the spinal cord is the exclusive organ of communication between the brain and the periphery, a complete loss of sensibility, voluntary motion, etc., following its division, compression, or disorganization, there still prevails some uncertainty as to the exact routes by which afferent impressions made upon the periphery are transmitted from the posterior roots through the cord to the brain and efferent impulses in the reverse direction through the anterior roots to the periphery.

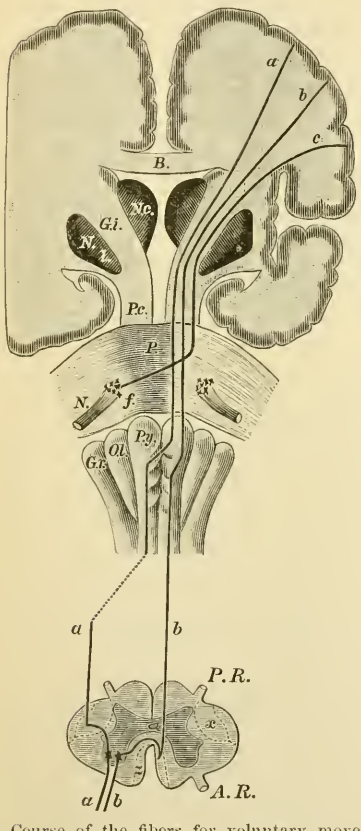
The difference of opinion held in this respect by physiologists, the diametrically opposed views that have been maintained, are no doubt due partly to the fact of the structure of the spinal cord not yet being thoroughly understood either in man or animals, but also in a great measure to the conclusions based upon experiments performed upon animals being applied to man without it being taken into consideration that not only does the spinal cord of animals dif-

fer in certain respects from that of man, but that it varies in its structure in different parts of its course even in the same animal.

Pathways of Afferent and Efferent Impulses in the Cord.

It has just been shown by histological investigations that a continuous tract of nerve fibers exists (Fig. 322), extending from the cerebral cortex, *ab*, through the corona radiata, internal capsule, (*Gi*), crus, pons (*P*), and which arriving at the medulla traverses thence as the direct (*b*) and crossed pyramidal tracts (*a*), the anterior and lateral columns of the cord, the fibers of the tracts, or rather their relays, the spinal neurons, leaving the cord (Fig. 313) at different levels as the anterior roots to terminate in striated muscles. Such being the disposition of the fibers of the anterior and lateral columns of the cord in reference to the anterior roots and muscular system it might be inferred that the functions of these columns are to a great extent at least motor, subserving the transmission of voluntary impulses. That such is the case is shown by both experimental and pathological evidence. Thus if a section be made of the spinal cord of an animal,[1] a dog, rabbit, or guinea-pig for example, involving only the lateral columns, entire loss of the power of voluntary motion on the same side will be observed below the level of the section, while if the columns be stimulated at their distal ends, the muscles supplied by the portion of the cord below the section will be thrown into contraction.

Fig. 322.



Course of the fibers for voluntary movement. *ab*. Path for the motor nerves of the trunk. *c*. Fibers of the facial nerve. *B*. Corpus callosum. *Nc*. Nucleus caudatus. *Gi*. Internal capsule. *N*. Lenticular nucleus. *P*. Pons; *Nf*. Original of the facial. *Py*. Pyramids and their discussion. *Ol*. Olive. *Gr*. Restiform body. *PR*. Posterior root. *AR*. Anterior root. *x* crossed and *z* direct pyramidal tracts. (Landois.)

To avoid misunderstanding, it may be stated that the direct pyramidal tract exists only in man and the monkey, that it extends

[1] In making sections of the cord in an animal it is indispensable that the spinal column should be firmly fixed, and that the cord be divided within certain defined measurable areas. These conditions are fulfilled by using the instrument devised by Ludwig and Woroschiloff, and described in Ludwig's Arbeiten, 1875, s. 248.

in man only to about the middle of the dorsal region, and that it contains only from 10 to 20 per cent. of the fibers of the total pyramidal tract, the remaining fibers decussating with those of the opposite side as the crossed pyramidal tract. Further, as the vasomotor and sweat fibers traverse the lateral columns, leaving the cord by the anterior roots, division of those columns, as in the case of the experiment just described, will involve modifications of the blood supply and the production of sweat below the level of the section. Clinical and pathological facts also confirm the view that voluntary impulses are transmitted from the brain to the periphery by the pyramidal tracts. Thus, a clot in the internal capsule is followed by hemiplegia, or loss of voluntary power over the muscles of the opposite side of the body, the clot blocking the transmission of impulses from the motor areas of the cortex to the muscles. Further destruction of the motor areas of the cerebral cortex involves a secondary degeneration,[1] which progressing downwards invades successively the internal capsule, crus, pons medulla, anterior columns of the same side, and the lateral columns of the cord of the opposite side of the lesion, the nutrition of the fibers of the pyramidal tract being governed by cerebral cells, just as the fibers of the anterior roots are governed by spinal cells. As the direction in which a fiber degenerates, in the case of a motor nerve at least, is the same as that in which it conducts, it is inferred that the fibers of the pyramidal tracts are efferent in function, conducting motor impulses from the brain to the periphery.

It is interesting, in this connection, as offering an explanation of the fact that the movements of both halves of the body are controlled by one hemisphere, that, in cases of secondary descending degeneration of the cord, degenerated fibers have been found in both crossed pyramidal tracts, the pyramidal fibers appearing to divide into branches, "geminal fibers,"[2] one branch passing to the opposite side of the cord, the other continuing in the original direction on the same side. Although our knowledge of the sensory pathways in the cord is far less definite than that of the motor ones, both experimental and clinical investigation show that the fibers of the posterior roots, which cross the middle line of the cord and ascend in the anterior and anterolateral columns (Fig. 313, 4, 5), are those that convey afferent impulses to the sensory areas of the brain. Thus, for example, a hemisection of the cord made in a dog at the level of 3 (Fig. 323) is followed by loss of sensibility on the opposite side of the body and loss of voluntary

FIG. 323.

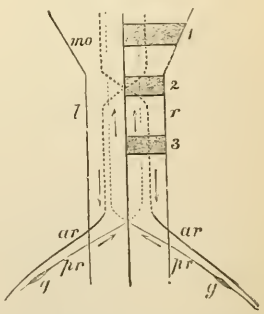


Diagram showing the course of the motor and sensory fibers in the spinal cord and medulla oblongata.

[1] Turck, Wiener Sitzberichte, 1851, s. 289. [2] Sherrington.

motion on the same side. If the section be made, however, at a higher level, as at 1 or 2, then the paralysis of both motion and sensation will be on the same side of the body, but on the opposite side to that of the section. It follows, also, that if the spinal cord be divided longitudinally below the medulla, that while the animal is able to stand on his four legs and make voluntary movements, as first shown by Galen,[1] it has lost all sensibility in them, all the sensory fibers being divided at their decussation in the middle line, the motor fibers remaining uninjured by the section.

Unilateral lesions of the spinal cord in man confirm the view, as learned from experiments upon animals, that the sensory pathways in the cord lie in the lateral columns. Thus, in the case reported by Gowers,[2] in which the lateral column and gray matter of the upper cervical region of the cord was wounded by a spicule of bone, entire loss of sensibility to pain was observed on the opposite side of the body.

While there can be but little doubt that the decussation of the sensory fibers in the spinal cord of man is complete, such does not obtain, to the same extent, in all animals, the decussation being much less complete in mammals, reptiles, and birds than in man, and less in the lumbar than in the dorsal portions of the cord in certain animals. In connection with the anæsthesia of the opposite side of the body following a hemisection of the cord may be here appropriately mentioned the hyperæsthesia usually developed in the same side as that of the section. This remarkable condition of excited sensibility, made quite evident within a few hours after the operation by the movements of the animal made in response to the slightest pinching, etc., of the skin, and lasting often for weeks, is probably due to the increase in temperature and vascularity brought about by the division of the vasomotor nerves, or the nerves regulating the caliber of the blood vessels, which, we shall see hereafter, descending from the vasomotor center in the medulla oblongata through the antero-lateral columns, but is also, no doubt, to be attributed to the division of the inhibitory or restricting fibers, whose influence being lost, therefore, upon the parts below the section, the latter become more excitable, more susceptible to external stimulus,

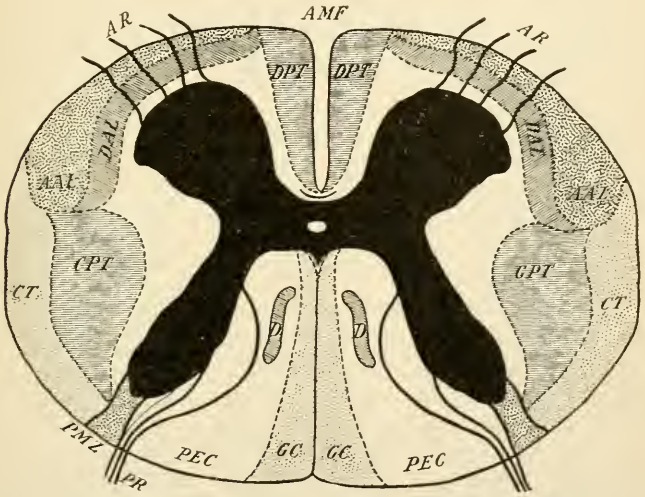
Attempts have been made by physiologists to prove that there exist in the cord distinct pathways for the impulses giving rise to the sensations of pressure, heat, and cold, entirely independent of those transmitting the impulses giving rise to pain. Even if such should prove hereafter to be the case, it is more probable that the above sensations, when sufficiently intense, give rise to pain than

[1] De Anat. Administrat, Lib. viii., Cap. v., Opera Omnia, T. ii., p. 683. Lips., 1821. Galen does not appear, however, to have observed the loss of sensibility in such cases, which was first observed by Fodera in 1822, Journal de Physiologie, T. iii., p. 199. Paris, 1823.

[2] Clinical Society's Trans., Vol. xi., 1878, p. 24. Since the above was written two cases of pistol-shot wounds have been reported by D. H. W. Cushing (American Journal of the Medical Sciences, June, 1898) which confirm still further the views expressed in the text as to the avenues of tactile sensations.

that special "specific" pain fibers exist in the cord. A very marked distinction exists, however, between general and tactile sensibility—the ability to feel, to appreciate—a sensation not necessarily enabling one to localize it. It would appear, therefore, that there must be distinct pathways for the transmission of impulses giving rise to tactile sensations and such seems to be the function of the fibers, already referred to, which, traversing the posterior columns of the cord, cross the middle line high up above the cuneate and clavate nuclei and pass to the opposite hemisphere. At least in cases like that described by Müller,[1] in which the whole of one-half of the cord and the posterior column of the other half was divided by a stab-wound; while loss of sensibility of pain was confined to the side opposite the lesion, loss of the sense of touch ex-

FIG. 324.



Transverse section of spinal cord, showing the degeneration tracts, and the paths that do not undergo degeneration in the cord. *AMF.* Anterior median fissure. *DPT* and *CPT.* Direct and crossed pyramidal tracts. *AR* and *PR.* Anterior and posterior roots. *AAL* and *DAL.* Ascending and descending antero-lateral tracts. *CT.* Cerebellar tract. *D.* Comma-shaped tract. *PMZ.* Posterior marginal zone. *PEC.* Column of Burdach. *GC.* Column of Goll. The parts left white do not undergo degeneration. (LANDOIS.)

isted on both sides. It may be mentioned, as confirming the view that the avenues for tactile sensation lie in the posterior columns of the cord, that in the case of Gowers, just mentioned, in which the posterior column was only œdematous, tactile sensibility was unimpaired.

While unilateral lesions of the spinal cord, such as those just mentioned, show that in man at least the paths for the conduction of all forms of sensory impulses decussate in the cord, clinical and experimental investigations prove that the paths for the impulses from the muscles lie in the columns of Goll (*GC*, Fig. 324), of the same

[1] Beiträge zur Path. Anat. u. Phys. der Rückenmark, 1871; Köbner, Deut. Arch. f. klin. Med., Band xix., 1877, s. 190.

side of the cord. Thus, if the posterior roots be attacked by disease, as in locomotor ataxia, or divided experimentally in animals, the secondary degeneration so arising will be ascending, will progress centripetally along the nerve roots to the cord upwards through the so-called Lissauer's zone in Burdach's column (*PEC*) for a short distance, and passing thence into the columns of Goll (*GC*), will ascend on the same side of the cord to the clavate nucleus of the medulla. It is an interesting fact that disease of the columns of Goll is followed by defect of muscular coördination, resembling so closely that due to disease of the cerebellum as to admit of no doubt that the impulses determining cerebral coördination pass from the muscles by the columns of Goll to the clavate nucleus of the medulla, and thence by relay fibers through the cerebellum to the cortex.

Fig. 325.

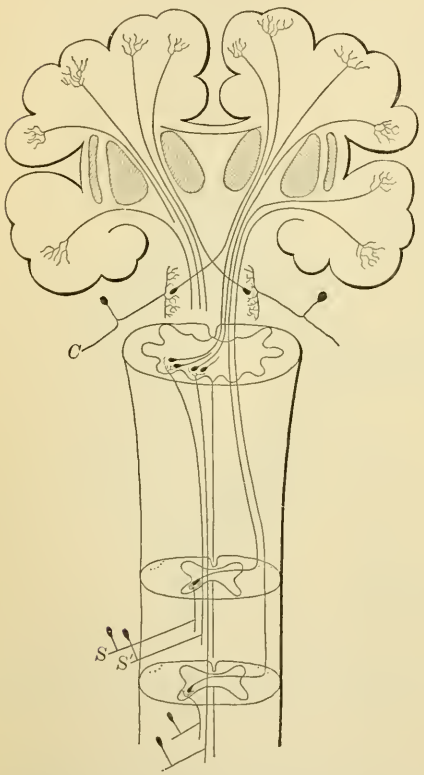


Diagram showing pathway of the sensory impulses. On the left side *S S'* represent afferent spinal nerve fibers; *C*, an afferent cranial nerve fiber. These fibers terminate near central cells, the neuron *S* of which cross the middle line and end in the opposite hemisphere. (Van Gehuchten.)

If the disposition of the sensory tracts be such as just described, it will be observed that the sensory resemble the motor tracts in that, of the two sensory tracts, one, the sensory, crosses the middle line of the cord at all levels, the other, the tactile, at the medulla in black, just as, of the two motor tracts, one, the direct pyramidal, crosses the middle line of the cord at all levels, the other, the crossed pyramidal tract, at the medulla in block.[1]

That such is the case is further shown by the fact that division of the columns of Goll in animals is followed by defects of coördination similar to that due to loss of the cerebellum. While the function of the direct cerebellar tract (Fig. 324, *CT*) cannot yet be said to have been demonstrated, the fact of its fibers passing by way of the restiform body to the middle lobe of the cerebellum and thence by the superior peduncle to the opposite hemi-

[1] Van Gehuchten, Anatomie Du Systéme Nerveux De L'Homme, Deuxieme Edition, 1897, p. 758.

sphere, render it highly probable at least that they also convey impulses from the muscles of the lower part of the trunk, and from between the trunk and the lower limbs, and possibly from the viscera. That the fibers of the direct cerebellar tract are at least centripetal in function, convey impulses from the periphery to the brain, is shown by the fact that secondary degeneration, when arising in this tract, ascends to the medulla. In addition to the fibers, already described, that pass continuously from the posterior roots to the columns of Burdach, to the columns of Goll, the columns of Burdach contain short vertical fibers connecting apparently the gray matter of the posterior cornu at different but adjacent levels, which possibly have a commissural or coördinating function. It may be here mentioned that if such be the case it is quite possible that those portions of the anterior columns not containing the efferent fibers of the anterior roots, may have similiar functions. Of the functions of the remaining tracts of the cord, still undescribed, the ascending antero-lateral tract (Fig. 324, *AAL*) of Gowers and the descending antero-lateral tract (*DAL*), and the so-called comma tract (*D*) in the column of Burdach, little or nothing is known. That the ascending and descending antero-lateral tracts convey impulses from the periphery to the brain and the brain from the periphery respectively, is shown by the fact that secondary degeneration arising in these tracts progresses centripetally in the former and centrifugally in the latter. It is possible, therefore, that sensory impulses may ascend in part through the ascending antero-lateral tract of Gowers. The descending comma tract hardly deserves the name of a tract, extending but a short distance through the cord after section, and consists probably of fibers of the posterior root, which take a descending course after entering the cord. That the spinal cord consists of tracts, such as those just described, is further proved by the manner in which the cord develops. Thus it has been shown by Flechsig[1] that the fibers of the cord get their covering of myelin at different periods of development, the fibers having the longest course becoming medullated latest.

In conclusion it will be seen from Fig. 324 that there still remain areas of fibers (unshaded) which do not degenerate after section, injury, or disease of the cord, and whose functions have not as yet been determined. It must be mentioned in connection with what has been said as to the result of division and disease of different parts of the spinal cord, that, from the fact of the loss of the power of voluntary motion and sensation being frequently restored, there must exist potentially, so to speak, a vicarious power of interchange of function between different parts of the cord, certain fibers being capable of assuming the transmitting of sensory and motor impulses in addition to their ordinary functions. Although the distribution of the spinal nerves will be found in any treatise on anatomy a brief résumé of the same is here offered as illustrating their general

[1] Die Leitungsbahnen im Gehirn und Rückenmark des Menschen, 1876.

functions. It should be borne in mind that the branches of the spinal nerves, whether anterior or posterior, are in their functions mixed nerves, possessing both motor and sensory properties. The anterior branches of the four upper cervical nerves form the cervical plexus, and the four lower cervical, together with the first dorsal nerve, the brachial plexus. From the cervical plexus are derived the superficial cervical, great auricular, small occipital, supraclavicular, and phrenic nerves, and muscular branches; the brachial plexus supplying mainly the upper extremity, but giving off, also, the supra- and subscapular and thoracic nerves. The posterior branches of the cervical nerves, with the exception of the first, after passing backward from the vertebral canal, divide into external and internal branches, and supply the muscles and integument behind the spinal column, the posterior branch of the first cervical issuing between the arch of the atlas and the vertebral artery, being distributed to the contiguous straight, oblique, and complex muscles.

The anterior branches of the dorsal or thoracic nerves, with the exception of the last one, pass outwardly in the intercostal spaces, as the intercostal nerves, the anterior branch of the last dorsal, being situated below the last rib, crosses the quadrate lumbar muscle as it advances between the internal oblique and transverse muscle in a similar manner as an intercostal nerve. In their course the intercostal nerves, as they supply the muscles, give off lateral cutaneous branches, that from the second intercostal or the intercosto-humeral nerve being an important one, since it extends across the axillary space, running in juxtaposition with the small cutaneous nerve from the brachial plexus, and supplies the skin on the inner part of the arm. The posterior branches of the dorsal nerves, like those of the spinal nerves generally, after turning backward between the transverse processes of the vertebræ, divide into external and internal branches, the former supplying the skin contiguous to the angle of the ribs, the longissimus and sacro-lumbar muscles, the latter the skin over the spinous processes of the vertebræ, the multifid and semispinal muscles. The anterior branches of the upper four lumbar nerves, together with a filament from the last dorsal nerve, constitute the lumbar plexus, and which, after supplying the psoas and quadrate lumbar muscles, give off the ilio-hypogastric, ilio-inguinal, genito-crural, external cutaneous, obturator and anterior crural nerves. The posterior branches of the lumbar nerves pass backward, like those of the dorsal, to supply the longissimus and sacro-lumbar muscles, and the adjacent skin. The anterior branches of the upper four sacral nerves, together with the fifth and part of the fourth lumbar nerves, form the sacral plexus, from which are derived the filaments supplying the pyriform, internal obturator muscles, etc., the levator and sphincter ani, the superior gluteal, pudic, and great and small sciatic nerves. The sacral, together with the lumbar plexus, give off the nerves supplying the lower extremity. The anterior branch of the fifth sacral, a small

nerve, emerges from the end of the vertebral canal, and divides into two branches, one of which passes with a filament from the fourth sacral to end in the sympathetic, the other joining the coccygeal nerve. While the posterior branches of the upper four sacral nerves pass out of the vertebral canal by the corresponding sacral foramina, the posterior branch of the fifth sacral emerges from the end of the vertebral canal and together with the posterior branch of the coccygeal nerve supplies the skin and muscles of the back. The anterior branch of the coccygeal nerve also passes out of the end of the vertebral canal, is joined by a branch from the fifth sacral after perforating the coccygeal muscle and the great sacro-sciatic ligament, and terminates in the skin of the buttock. The posterior branch of the coccygeal, like the anterior branch, emerges from the end of the vertebral canal; its distribution has just been referred to in connection with that of the posterior branch of the fifth sacral.

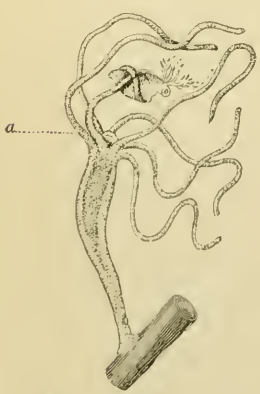
CHAPTER XXXI.

THE NERVOUS SYSTEM.—(*Continued.*)

DIVISION OF LABOR IN ANIMALS AND MAN. REFLEX AUTOMATIC AND NUTRITIVE FUNCTIONS OF SPINAL CORD.

One of the most striking differences in the organization of animals is the extent to which the division of labor, physiologically speaking, is carried. Indeed, the lowest forms of life, such as the monera, consisting, as we have seen, of mere masses of protoplasm, are so utterly unorganized as to make it impossible to say whether such beings should be assigned genealogically to the vegetable or animal kingdom. It is true, that among such primitive forms of life there are beings, like the common amœba, in which there is a slight differentiation of structure, in that not only a nucleus and nucleolus are present, but even an enveloping membrane or cell wall may be developed, and that among the infusoria are also seen forms, like paramœcium, apparently quite organized; nevertheless, even these protozoan animalculæ, so much more complex in their structure than the monera, cannot be said to be organized in the same sense that the remaining members of the animal kingdom, or metazoa, are. Even the infusoria, apparently complex as they are in their structure, are morphologically only unicellular, and never passing beyond this primitive one-celled stage; tissues, and still less organs, are never developed in them similar to those of which the body of one of the higher animals is made up, since, as we have already seen, the organs in the latter consist of tissues and the tissues of cells, the latter resulting from the division of the primitive cell. Indeed, it is not until we reach in the tree of life the porifera, actinozoa, and hydrozoa, of which the sponge, anemone, and jelly fish, familiar objects at the sea-shore, are examples, that we meet with anything like organization, at least in the true morphological sense of the word—that is to say, of an animal consisting of organs, made up of tissues, developed out of cells resulting from the segmentation of a primitive cell, or ovum. Suppose that the structure of one of the hydrozoa be considered, as that of the common green hydra (Fig. 326), found during the summer in almost every fresh-water

Fig. 326.

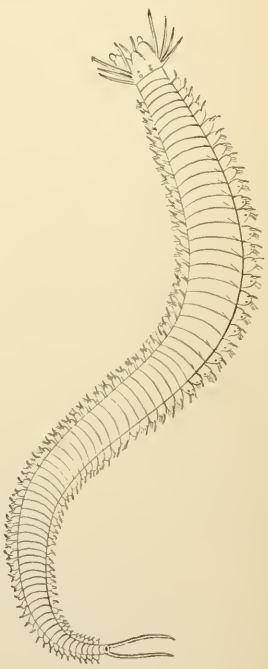


Hydra. (Milne Edwards.)

pool, and therefore an object for study accessible to all, it will be found that the animal, about half an inch in length and a line in diameter, is essentially a double-layered tube, closed at one end and open at the other, the latter serving as a mouth and surrounded with delicate tentacles, or feelers, by means of which it seizes its prey, the outer layer, or ectoderm, of the tube, functionating as skin, the inner layer, or endoderm, as a mucous digestive surface.

Leaving out of consideration an imperfectly developed neuro-muscular layer or mesoderm intermediate between the ectoderm and endoderm (absent in the protohydra), the hydra may be considered functionally as little more than a digestive sac. That the differentiation of ectoderm and endoderm is very incomplete, is shown from the fact that if the animal be turned inside out the skin or ectoderm becomes digestive in function, and the digestive surface or endoderm epidermal, just as the mucous membrane of the mouth or anus in man may become skin if everted, or the skin of the same parts mucous membrane if inverted. This is, however, as might have been expected, since, as we shall see hereafter, there can be little doubt but that the ectoderm and endoderm of the hydra are homologous with the epiblast and hypoblast of the embryo, or the parts corresponding to the skin and mucous membrane of the adult. Further, that no one part of the hydra differs essentially from any other part, is shown by the well-established fact that if a hydra be cut up into several pieces each piece will live and lead an independent existence and develop into a perfect hydra. While, at first sight, such a result may appear as a very extraordinary one, it becomes a perfectly natural and intelligible one when it is remembered that all parts of the body of the hydra have essentially the same function, and that there is no interdependence between the parts of which it consists. Reproduction by fission, whether produced artificially or naturally, is not confined, however, by any means to such low forms of life as the hydra, being observed as well in quite highly organized animals, as among the annelida, of which the marine worms, such as the clam worm (Nereis pelagica) of our coasts (Fig. 327), etc., are examples. The body of a nereid worm, consisting of numerous segments, is naturally very apt to break up into numerous pieces consisting of one or more of the segments, as the animal glides along among the rocks, sand, or seaweed, each piece becoming, under favorable circumstances, a perfect animal. In-

FIG. 327.



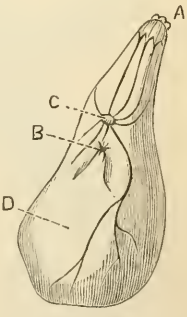
Clam worm. Nereis pelagica.

deed, at certain seasons of the year there may be seen in certain kinds of these worms (Protula) at different portions of the body constrictions indicating the parts where the body will break up, by natural fission, into a progeny of worms. That such a mode of reproduction should take place in an animal as highly organized as those just mentioned, having a distinct body cavity inclosing a nervous system, alimentary canal, heart, may appear even more extraordinary than the case of the hydra just referred to. It must be borne in mind, however, that in the worm, as in the hydra, there is but little interdependence of parts, each segment having its own nervous ganglion and fractional part, so to speak, of the alimentary canal and vascular tubes running from end to end of the animal. In fact, an annelid may be regarded, morphologically, as consisting of a chain of small annelids (the segments depending but little upon each other, linked together, as it were, for only the time being). A glance now at the organization of a vertebrate animal, or even one of the higher invertebrates, will at once show how profoundly such an animal differs from any of those hitherto mentioned. The brain, as in man, for example, situated in the skull, depending for its activity upon the blood driven to it by the heart in the thoracic cavity, the rhythmical action of the heart and lungs maintained by nervous influences emanating from the base of the brain, the alimentary canal within the abdominal cavity supplying the materials for the nourishment of the brain and other organs, but dependent upon the blood supplied to it by the heart for the elaboration of the alimentary secretions, illustrating sufficiently how intimate is the connection existing between the cranial, thoracic, and abdominal organs, and the impossibility of any one segment of the body containing such, living a life entirely independent of the remaining ones, as we have just seen is the case in many of the lower animals. This contrast between the lower and higher animals with reference to the extent with which the division of labor is carried on, is well illustrated by the difference between the savage and civilized state of society—and, indeed, the difference is something more than a mere comparison, being of a profound meaning to those who believe that the life of a nation is developed according to law as certainly as that of the individuals of which it is composed.

In the uncivilized, savage state, each individual is independent of his neighbors as the one segment of the worm may be to that of the other; his interest not being usually their interest—on the contrary, often antagonistic—he builds his simple hut, hunts his own game, clothes himself; a birth among his tribe adds to, a death takes away nothing, from his daily life. Under such circumstances there can be no accumulation of wealth and the development incidental to it. In the civilized state, on the contrary, the interest of the one is the interest of all, as that of the one organ in the human body is that of the others; each individual confining himself to one avocation, the latter is advanced to its utmost limits, depending upon others for that which he does not produce himself, the

product of his own industry reaches the highest perfection ; and so with the productions of others, and thus the wealth of the nation increases both in variety and amount. Just as with the uncivilized, as compared with the civilized, so with the lower animals as compared with the higher ones ; just as the development of a nation depends, not only upon the variety of the interests, but upon the mutual interdependence of the same ; so the life of an animal is high in proportion to the variety of its organs, and the mutual harmonious working of the same. The famous example of the number of persons engaged in the making of nails or pins, and the great number that can, consequently, be so produced, as mentioned by Adam Smith,[1] is as applicable as illustrating biological as well as politico-economical laws. The life of a man biologically as well as socially, when compared with that of a sponge, may be summed up in saying that in the former the division of labor is carried, so far as we yet know, to its utmost limits ; in the latter but little, if at all. This division of labor, so characteristic of the higher animals, and which we have illustrated on account of its importance somewhat in detail, is not only well seen in the general organization of the higher animals, but in the extreme differentiation exhibited in their alimentary, vascular, nervous systems, etc., and as it is the functions of the latter that we are now more particularly considering, it will be well to illustrate the general structure of the nervous system in animals by a few examples before taking up the consideration of the subject of the reflex action of the spinal cord of man, the nature of which it is hoped will be made clearer by the preceding introductory than it would have been without it.

Fig. 328.



Nervous system of an ascidian. A. The mouth. B. The vent. C. The ganglion. D. The muscular sac.

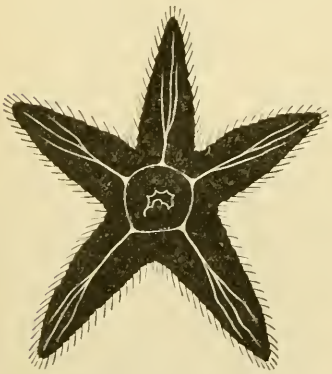
Of the simplest form of nervous system may be mentioned that of the ascidioida, as seen, for example, in a phalusia, in which the entire nervous system consists (Fig. 328) of a single ganglion, receiving or giving off filaments from or to the periphery. On touching this worm-like animal, and seeing it contract its body, judging from one's own feelings and actions, we would infer that the animal felt the touch and voluntarily retracted its body, and conclude that the impression made upon the integument was transmitted by an afferent centripetal, or sensory nerve, to the ganglion, and there felt, and that the impulse emanating from the latter was transmitted by an efferent, or centrifugal, or motor nerve to the muscle, and there resulted in voluntary motion, the whole action being called a reflex one from the fact of the impression made upon the periphery being first transmitted to the ganglion and thence reflected back again. If the ganglion be not endowed with sensation

[1] An Inquiry into the Nature and Causes of the Wealth of Nations, Vol. i., p. 7. Edinburgh, 1814.

and volition, then the animal must be without either, since it possesses no other structure of which such qualities can be predicated. Further, if muscular action, in response to stimuli applied to the periphery, is no evidence of either sensation or volition, then it is impossible to say whether any animal feels, or wills, under any circumstances. If now the nervous system of a starfish be compared with that of the ascidian, just mentioned, the only essential difference presented by the former is that, instead of one ganglion there are five (Fig. 329), which, together with the commissural filaments, constitute a circum-oral ring, from which are given off the nervous filaments supplying the rays.

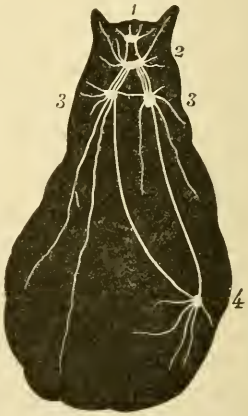
It follows, therefore, that if the ganglion of the ascidian be endowed with sensation and volition, then all five ganglia of the starfish are endowed with the same functions, the only difference between the two being that, in the one, whatever sensation and vo-

FIG. 329.



Nervous system of starfish. (DALTON.)

FIG. 330.

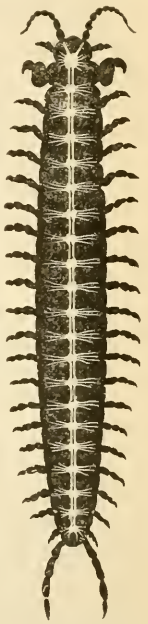


Nervous system of aplysia. (DALTON.)

lition the animal may be possessed of is concentrated in the single ganglion, whereas, on the other, the sensation and volition are diffused among the five ganglia. It is obvious, also, that, on account of the radial symmetry presented by the starfish, it is impossible to assign any special function to any one of the ganglia that is not possessed by the others. And, while even in the mollusca, of which the aplysia (Fig. 330), or sea hare, is an example, the supra-œsophageal ganglion (1) is regarded, morphologically, as a brain, there is little reason to suppose that it possesses, exclusively, any very specialized function not shared by the infra-œsophageal (2) one, or that the latter, in turn, differs very much, functionally, from the remaining ganglia (3, 4) distributed through the body, and with which it is connected by a commissural filament as well as with the supra-œsophageal one. It is true also, that the supra-œsophageal ganglion (Fig. 331) of centipedes, insects, etc., is usually spoken of as the brain of such animals, and the ventral chain

of ganglia compared to the spinal cord of vertebrates, but, as some of the nerves in insects, for example, supplying the head, are derived from the supra-œsophageal ganglion, and others from the infra-œsophageal ganglion and, as the latter ganglion does not differ essentially from the remaining ones of which the ventral chain consists, it is difficult to see why any one ganglion should be designated as cerebral and the other as spinal. That there is no such essential difference between the so-called cerebral and spinal ganglion is shown from the fact that, if a worm breaks up into two, through fission, the ganglion that was central in the parent animal becomes anterior in the new individual, and goes to form its brain. Further, in the case of worms, insects, etc., it is questionable whether such animals are comparable at all as regards their nervous systems with vertebrated ones, since, as a glance at Fig. 332 will show, while the cerebro-spinal nervous centers of the vertebrate are dorsal, the ganglion chain of the articulate is ventral, and, while the heart is dorsal in the articulate, it is intermediate in the vertebrate between the alimentary canal and the nervous center. In other words, to compare an articulated with a vertebrated animal, with reference to homologizing their nervous systems, one or the other must be placed upside down, and, however the vertebrated animal be placed, it is obvious that no comparison can be made at all between its nervous system and that of the echinodermatous or molluscous type. Such being the case, it would be illogical to apply the results of investigation made upon the nervous system of invertebrates to that of vertebrates, the nervous system not being comparable in the two great divisions of the animal kingdom. For this reason, any conclusion as to the functions of the different parts of the nervous system in man, drawn from the study of the nervous system in animals, must be based upon that of the vertebrates only, more particularly of such classes in which the parts composing the nervous system can, without doubt be homologized. The amphioxus, the lowest of vertebrates, being practically headless, offers, in the structure of its nervous system, little or nothing comparable with the brain of the remaining vertebrates. Unless it be denied that the amphioxus can feel or will, of which there is not the slightest evidence, it necessarily follows that the spinal cord of this primitive vertebrate, at least, is endowed with sensation and volition. If such be admitted, and it is difficult to see how the conclusion can be avoided, analogy would lead us to suppose that the spinal cord of the lamprey and myxine, to a certain extent, at least, would possess, also, similar qualities, particularly as the sensation and volition exhibited by such animals are

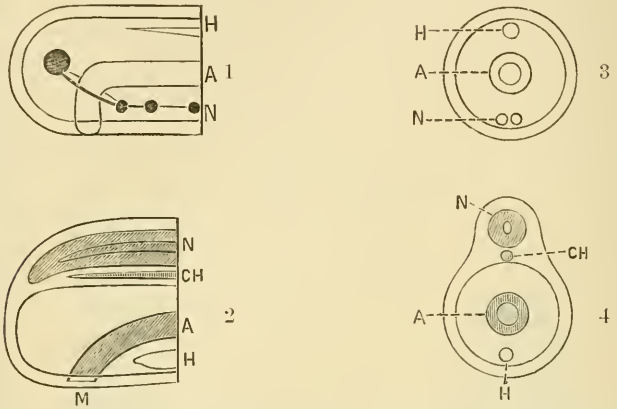
FIG. 331.



Nervous system of centipede. (DALTON.)

out of all proportion to the amount of brain present. Inasmuch, however, as these marsipo-branchial fishes have a brain, or, at least, the basal ganglia of the brain of the higher vertebrates, it is to be inferred, that with these additional important structures, even if little developed, there would be exhibited corresponding higher faculties than shown by the amphioxus, and such is found to be the

Fig. 332.



Diagrammatic sections of an articulated invertebrate and vertebrate. 1. Longitudinal section of invertebrate. 2. Longitudinal section of vertebrate. 3. Transverse section of invertebrate. 4. Transverse section of vertebrate. H. Heart. A. Alimentary canal. N. Nervous system. CH. Chorda dorsalis.

case, and as we pass from these lowly organized vertebrates through the higher ones, to man, it will be observed that the brain becomes more and more developed both relatively and absolutely with reference to the spinal cord, the extremes of the series being represented by man and the amphioxus respectively.

Ratio of Brain to Spinal Cord in Vertebrates.

Man	33.0 to 1
Mouse	4.0 to 1
Pigeon	3.3 to 1
Triton	0.550 to 1
Lamprey	0.001 to 1
Amphioxus	0.0 to 1

Now, as we have seen in general that the higher animals differ from the lower ones in the extent to which the division of labor is carried, the higher grade of life exhibited by the former depending upon the greater differentiation of their organization, the development of the brain just alluded to might have been anticipated, it being obviously of advantage that certain functions of the nervous system would be restricted to the brain, others to the spinal cord, and hence, as we shall see presently, the great development of the intellectual powers in the higher animals as compared with the lower ones. Further, it will be found that corresponding with this idea of the division of labor, that while the spinal cord of the lower vertebrates may possess both sensation and volition, that of the

higher ones in becoming to a considerable extent a conductor of sensory and motor impulses loses such qualities, the seat of the sensorium and will being transferred to a higher plane, being gradually elevated, so to speak, in the higher animals. Thus, while sensation and volition are diffused through the spinal nervous axis of the lowest vertebrates, it gradually, through the process of development, becomes concentrated in the cranial expansion of that of the higher ones. The theoretical considerations just offered are fully borne out by experiment as well as by the facts of comparative anatomy. Thus, if a frog be decapitated and a drop of acetic acid be placed upon the skin near the anus [1] the animal keeps changing its position, and will endeavor to wipe off the acid by means of the foot of the same side of the body to which the acid was applied, and, if the latter be amputated, by means of the opposite foot. Not infrequently, also, the author has seen the animal try to remove the acid by one of the upper extremities, both legs having been amputated. Considerable difference of opinion still exists as to whether such an action as that exhibited by a decapitated frog involves sensation and volition, or is to be regarded as a simple reflex action—that is, of an action such that an impression being made upon the skin of an animal and being transmitted by an afferent nerve to the gray matter of the cord, is thence reflected by an efferent nerve to a muscle without the animal necessarily feeling anything or making any voluntary effort. It appears to us, however, that a frog with its head on when stimulated by acetic acid gives but little more evidence of sensation and volition than with its head off when so stimulated, the difference exhibited between the cases being rather one of degree than of kind. Of course, the frog with its head on feels and wills more than with its head off, but it does not follow, in the latter case, that the animal does not feel or will at all. Indeed, if it be denied that the decapitated frog feels and wills, it becomes very questionable whether there is any way at all of positively proving that the frog with its head on feels and wills. Further, if it be affirmed that sensation and volition are restricted to the brain, then the amphioxus must be without either, and that exhibited by the lower vertebrates, the frog included, out of proportion to the amount of brain present. It is often urged that, as we know from cases in which the spinal cord has been injured in man, that muscular contractions resulting from the tickling of the sole of the foot are performed unconsciously, that the muscular action just described as taking place in the decapitated frog is no evidence that the animal either feels or wills. It should be borne in mind, however, that no one ever saw a man with a fractured spine, still less with his head cut off, apply his hand or foot to his anus and wipe away acetic acid placed thereupon, as done by the decapitated frog, and until this has been observed it can hardly be said that the cases are parallel, or that conclusions can be drawn as to the sensation or volition possessed by the spinal cord of the decapitated frog from ob-

[1] Pflüger, Die Sensorischen Funktionen des Ruckenmarks, 1853.

servations made upon human beings suffering from injuries of the spine by tickling the soles of the feet. Indeed, the muscular contractions following the tickling of the sole of the foot in cases of injuries of the spine in human beings are very simple in character, similar to those ensuing when the nerve of an amputated limb is stimulated, whether it be that of a man or frog.

Such contractions are never coördinated with reference to the performance of any definite object, and do not suggest in any way the idea that the amputated limb either feels or wills, and the case is not substantially altered by the limb being attached to the body, the only difference being then that the nerve is bent into an afferent and efferent arc, the gray matter of the cord connecting the axis-cylinder of the ascending and descending parts of the same. The question may never be settled as to whether the headless frog feels and wills or not, or to what extent sensation and volition may be properties of the spinal cord in the lower vertebrates. Indeed, nothing short of being a frog would give us positive assurance that such an animal possesses consciousness as Professor Huxley observed in considering the same point in reference to the crayfish.[1]

On the supposition, however, that man has gradually developed, and in harmony with the idea that as we pass from the lower to the higher vertebrates through the division of labor, the properties of the spinal cord from being general, become more and more special in character, it is quite possible that many actions which are now performed unconsciously in the higher animals may have been originally accompanied with both sensation and volition in the lower ones, and to a certain extent are still. As a matter of fact, many actions like that of walking, playing upon musical instruments, etc., involving at first both sensation and volition, through constant repetition are performed in time unconsciously. Whether this view of all reflex action being originally accompanied with consciousness, but through constant repetition being finally performed unconsciously, becoming, as it were, organized within us, a kind of second nature, be accepted or not, there is no doubt that in man, at least, that the seat of sensation and volition is limited to the brain, and that there are many and varied actions going on in the body not involving consciousness at all, and performed entirely by the spinal cord and medulla, to the consideration of which let us now turn.

A reflex action (Fig. 333) implies the presence of an afferent or centripetal nerve (*A*) of the gray matter of the cord (*C*), and of efferent or centrifugal ones (*E E*). We make use of these terms in preference to those of sensory and voluntary motor nerves, since many reflex actions like the rhythmical action of the heart and lungs are performed entirely unconsciously without our feeling or willing in the matter at all, while others, involving sensation, as the winking of the eyelids on an object being brought suddenly close to the eyes is entirely involuntary, as we all know from daily experi-

[1] The Crayfish, 1880, p. 89.

ence. In many instances of reflex action, as in deglutition, walking, coughing, sneezing, tetanus, vomiting, etc., both the afferent and efferent nerves involved are cerebro-spinal nerves. In other cases, as in blushing, etc., while the afferent nerves are cerebro-spinal, the efferent nerves belong to the sympathetic system. On the other hand, the afferent nerves may be derived from the sympathetic, the efferent from the cerebro-spinal system, as in convulsions due to the

Fig. 333.

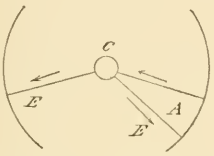


Diagram to illustrate reflex action.

Fig. 334.

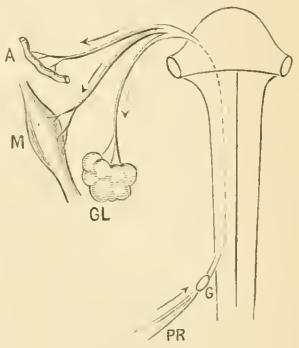


Diagram to illustrate reflex action of medulla.

presence of intestinal worms, not uncommon in infants. Finally, both afferent and efferent nerves may be sympathetic nerve fibers, as in the production of certain of the intestinal secretions. Whether, however, the afferent and efferent nerves be cerebro-spinal or sympathetic in origin, or the phenomena be accompanied with sensation, but without volition, or without either, in each of the instances just referred to, an impression being made upon the periphery and transmitted by an afferent nerve to the gray matter of the cord is thence reflected outwardly again to the periphery by an efferent one. Further, while muscular, glandular, or vascular action may follow an afferent irritation according as the efferent nerve is distributed to muscle, gland, or vessel, as in the instances just given, it is not impossible that all three effects may be produced simultaneously by a single impulse, as in the case illustrated by Fig. 334.

Many of the examples just given being rather illustrations of the reflex action of the medulla than of the spinal cord, their further consideration will be deferred until the afferent and efferent nerves have been described.

If the impression made upon the periphery be not a very strong one, usually the reflex action resulting is unilateral—that is to say, is confined to the same side of the body irritated. If, however, the impression be sufficiently strong to pass through the gray matter of the cord and be reflected outwardly, then the reflex action is symmetrical—that is, the general effect produced on the opposite side of the body is the same as that of the side irritated. As might be expected, if the impression be sufficiently strong to produce the same effect on both sides of the body, the movements upon the opposite side never surpass in extent those of the side irritated. Further, while the efferent nerve excited is usually on the same plane as

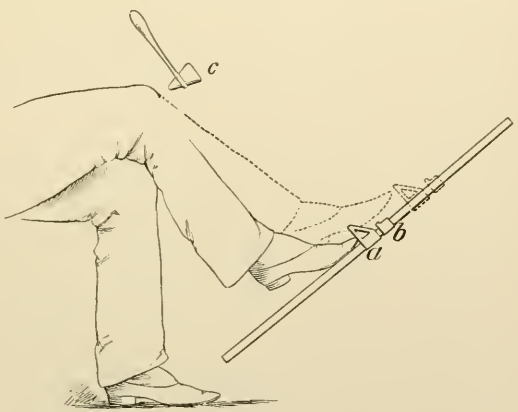
that of the afferent one irritated, if the impression be sufficiently strong, the nerves excited are always situated above, and never below, that plane. It should be mentioned, however, in this connection in the case of the reflex action of the encephalon the impression passes downward to the medulla oblongata. It is also well known that a single weak stimulus, incapable in itself of causing a reflex action, may do so, however, if repeated sufficiently often. The piling up or "summation of the stimuli," as it is called, appears to take place in that part of the spinal cord situated between the terminal twigs of the afferent nerves and the cells. Some difference of opinion exists as to the number of stimuli necessary to elicit a reflex response. It would seem, however, that while 3 feeble stimuli per second will cause reflex action, 16 stimuli per second are much more effective. A certain period of time, the so-called "period of latent stimulation," elapses between the application of a stimulus and the reflex response. In the case of a pithed frog, dilute sulphuric acid being used as the stimulus, and the latent period being the time elapsing between the application of the stimulus to the foot and the withdrawal of the latter, it has been shown that the latent period diminished as the strength of the solution is increased. It is also well known that the interval of time elapsing between the application of the stimulus and the response varies within wide limits. Thus in making use of electricity as a stimulus it has been shown[1] that the number of stimuli remaining constant, the latent period may vary from 0.05 to 0.4 second. It would appear, of the time elapsing between the application of the stimulus and the reflex response in the frog, that from 0.008 to 0.015 second is applied to the transferring of the impulse from the afferent fiber to the cell in the cord and from the latter to the efferent fiber, the time so consumed being known as "reflex time."[2] Reflex responses are much more readily elicited when the stimulus is applied to the specific end organ of the afferent nerve than to its trunk. Thus the reflex responses following the gentle tickling of the skin are much greater than those due to the stimulation of an exposed cutaneous nerve. It is well known that reflex action is increased by certain substances, and diminished by others. Of the former strychnia is the most powerful; an animal, a frog, for example, poisoned with strychnia exhibiting tetanic spasms on the application of the slightest stimulus. Of the latter may be mentioned chloroform, the bromides, etc.

That the different parts of the body are intimately connected has been well known from time immemorial to the physician, but it is only within comparatively modern times that it has been recognized that the sympathy, as it was called, undoubtedly existing between the various organs, depends upon reflex action. As the doctrine of sympathy is a very important one from a clinical as well as from a physiological standpoint, it may not appear superfluous to illustrate

[1] Ward, Du Bois Reymond Archiv Phys. Abthl., 1880, s. 72.
[2] Landois, op. cit., p. 809.

it a little by a few examples. Thus, for example, the œsophagus having been divided, if the stomach be irritated, the salivary glands will secrete; on the other hand, if the lingual nerve be stimulated as by the taking of tobacco, the stomach will secrete. Evidently the impression made upon the stomach in the first case is transmitted to the cord and thence reflected outwardly to the salivary glands, whereas in the second case the impression, being made upon the tongue, is transmitted to the cord and thence reflected to the stomach. Similarly, the irritation due to hemorrhoids modifies the character of the gastric juice to such an extent that digestion becomes impossible, and the ensuing dyspepsia only curable by removal of the hemorrhoids or the exciting cause. The flow of tears due to some external irritation disappears with the loss of sensibility, while photophobia, often attributed to irritation of the optical nerve, is in reality due to irritation of the fifth pair of nerves. The fact of disease in one eye often involving loss of the other illustrates the nervous sympathy existing between the two. Neuralgia of branches of the frontal nerve, due to caries of the teeth, is of frequent occurrence. The irritation, and even inflammation of the abdominal viscera following severe burns is well known to the surgeon. The stoppage of the heart brought about by blows on the epigastrium, the tetanus due to injuries of the thumb and big toe, the paraplegia from disease of the urogenital organs, the development of the mammary glands coincident with that of the fœtus are familiar examples of reflex action.[1]

FIG. 335.



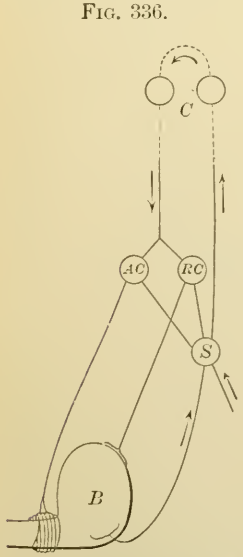
The knee-jerk.

The well-known "knee-jerk" (Fig. 335) elicited by striking the patellar tendon with the edge of the hand or a percussion hammer, the leg being semi-flexed, is specially interesting as an example of a deep tendon reflex, owing to the fact that it is increased or diminished by diseases, increased, for example, in lateral sclerosis, diminished or lost in locomotor ataxia.

[1] Brown Sequard, Central Nervous System, p. 153. Philadelphia, 1860. A. P. Brubaker, Reflex Neuroses, American System of Dentistry.

The above are illustrations among many that might be offered of the important fact never to be lost sight of, that the exciting causes of many physiological and pathological phenomena are to be sought for, not where the latter are exhibited, but frequently at a remote portion of the body, the impression made upon one organ being transmitted by an afferent nerve to the spinal cord, and thence reflected outwardly by an efferent one to where the phenomena are exhibited. If the various spinal nerves involved in the production of reflex actions be considered specifically, it will be found that just as the osseous spinal column is subdivided into osseous segments, so the spinal cord may be subdivided into nervous ones physiologically at least, the gray matter of which, according to this view, constituting so many reflex centers, and the spinal nerves the afferent and efferent nerves to and from the same. A number of such centers appear to have been satisfactorily made out, among which may be mentioned the cilio-spinal center, by which the dilatation of the pupil is effected, situated in the lower part of the cervical and upper part of the dorsal regions of the cord ; it will be considered again in connection with the sympathetic. The sweat and vaso-motor centers, whose influence upon the secretion of sweat and the blood vessels will be treated of hereafter. The ano-spinal center, governing the act of defecation, situated in the lumbar region, the afferent fibers being constituted by the hemorrhoidal and inferior mesenteric nerves, the efferent by the pudendal plexus, distributed to the sphincter ani muscle. The vesico-spinal center, both that governing the sphincter vesicæ and detrusor urinæ, being situated in the lumbar region of the cord.

Fig. 336.



Schema of micturition. *AC*, *RC*, *C*. Automatic, reflex, and cerebral centers. *B*. Bladder. *S*. Sensory center acted on by afferent impulses. (Landois.)

Two centers are assumed to exist in the cord, one, the automatic center (Fig. 336, *A C*), maintaining the tonic activity of the sphincter of the bladder, the other a reflex center (*R C*) exciting the fibers of the detrusor urinæ muscle, the urine-expelling fibers. Such being the disposition, afferent impulses from the sensory center (*S*) paralyze the automatic center and excite the reflex center, and so give rise to micturition. If the sensory impulses reach the cerebrum voluntary impulses descend which may aid or inhibit micturition, according as the automatic or reflex centers are stimulated.

The center for erection of the penis, lies in the lumbar region of the cord, the afferent fibers being the sensory nerves of the penis, the efferent ones the nervi erigentes. Stimulation of the latter, as we shall see here-

after, dilates the vessels of the penis. The center for the emission of semen is also situated in the lumbar region, the afferent nerves being the dorsal sensory nerves of the penis; the efferent, nerve fibers which, emerging with the fourth and fifth lumbar nerves, pass into the sympathetic, and are distributed to the vesiculæ seminales and vasa differentia, and with the third and fourth sacral nerves pass into the perineal nerves, and are distributed to the accelerator muscle. The center for parturition lies in the lumbar region, the afferent and efferent fibers consisting of part of the uterine plexus. From the fact of the reflex actions being stronger, and of less time elapsing between the application of the stimulus, and the resulting reflex when the spinal cord has been divided, it has been inferred that the encephalic centers exercise a restraining or inhibitory effect upon the reflex action of the cord. Thus, the spinal cord, being intact in a frog, and the average length of time elapsing between the application of the stimulus and the resulting reflex effect being determined, it will be observed that if the optic lobes, for example, be stimulated, a greater length of time elapses now than before between the stimulus and the reflex. On the other hand, the spinal cord being divided, less time elapses between the application of the stimulus and the reflex. While such experiments would lead one to conclude that in the frog the optic lobes contain a restraining or inhibitory center, Setschenow[1] center, it must not be supposed that the inhibitory influence of the encephalon is limited to the optic lobes in man. That there must be complex centers situated probably in the cortex of the brain by which the reflex action of the cord is inhibited, is shown by the manner in which we are able to restrain, for a time at least, the various functions performed by it, such, for example, as keeping the eyelids open when the eyeball is touched, arrest of movement when the skin is tickled, etc. It is held by many physiologists that the spinal cord not only exerts an automatic control over certain viscera, such as the rectum, bladder, etc., as just mentioned, but also over the skeletal muscles as well, maintaining the latter in a state of more or less tonic contraction. Of the facts offered among others as proving the existence of a muscle tonus, it has been urged that when a muscle is divided its ends retract. This effect appears to be due, however, not so much to loss of spinal control as to the fact that all muscles are more or less slightly stretched beyond their normal length. It is also well known that if the muscles of a decapitated frog be put on the stretch and the sciatic nerve divided the muscles do not elongate, a fact inconsistent with the idea of the muscles having been previously maintained in a condition of a tonus by the spinal cord. That a condition of reflex tonus may be brought about, however, is shown by the fact that if the decapitated frog be suspended in an abnormal condition it will be ob-

[1] Ueber die Hemmungsmechanismus für die Reflexthätigkeit des Rückenmarks, 1863.

served that while the leg in which the sciatic nerve has been divided hangs limp, the sound one is slightly retracted, the weight of the limb acting then as a stimulus. It should be mentioned in this connection that while there is no doubt that the spinal cord exerts automatic control over certain viscera and blood vessels (vascular tonus), the expression "automatic center" is a misleading one, as the so-called automatic centers differ only from other reflex centers in being stimulated at all times by blood or other stimulus, the ordinary reflex centers only temporarily. The spinal cord appears also as already mentioned to influence the nutrition of the tissues to which its nerves are distributed, the nutrition of the muscles being controlled by the anterior gray matter, and probably by the motor cells, that of the bones and joints being excited probably through the posterior roots.[1]

[1] Gower's Diseases of the Nervous System, Vol. i., 1892, p. 206.

CHAPTER XXXII.

THE NERVOUS SYSTEM.—(*Continued.*)

THE MEDULLARY NERVES.

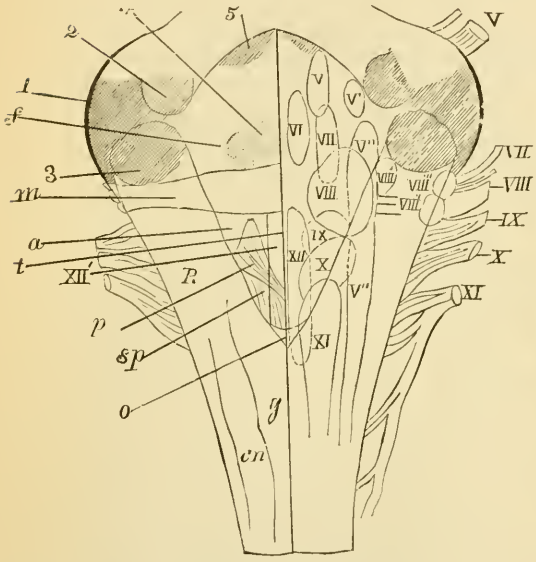
The medulla oblongata, regarded as a center of reflex action, is even more important than the spinal cord, on account of its giving origin to ten of the so-called cranial nerves—that is, of the nerves involved in the performance of mastication, insalivation, deglutition, of gastric and intestional digestion, circulation, and respiration—in a word, of the functions of nutrition. In order, however, to appreciate the manner in which these nerves conduct afferent and efferent impressions to and from the medulla, the latter acting as a reflex center, it will first be necessary to describe their origin, distribution, and function. From the fact of the medulla being simply the upper expanded portion of the spinal cord one would be led to suppose that the ten nerves originating in it would be either motor or sensory in function, and that taken together in pairs from below upward each pair would be comparable to the anterior or motor and posterior or sensory roots of one of the true spinal nerves. As a matter of fact, the roots of the two nerves of any one of the medullary pairs, supposing such to exist, do not unite together into a single nerve as in the case of a spinal nerve, but pass on separately to their ultimate distribution as two distinct nerves; and further, the reflex centers of the medulla oblongata, of which these nerves are the afferent and efferent fibers, are so fused together in man and the higher vertebrates that the primitive disposition of these centers and the relation of the nerves originating in them are no longer apparent. In fact, the union is so intimate that it is impossible to say now how many such nerves or roots there were originally, and until that is determined it will be impossible to homologize the medullary with the true spinal nerves. Indeed, until the development of the cranial nerves in the mammalia has been thoroughly worked out by the embryologist, and the relations between the cranial and spinal nerves in some of the lower vertebrates been established by the comparative anatomist, any view yet offered may be considered as based upon little more than speculation.[1]

Twelve pairs of nerves are given off from the base of the brain. The first two pairs, the olfactory and optic, the special nerves of the sense of smell and sight, are, as we shall see hereafter, morphologically outgrowths of the anterior cerebral vesicle; the

[1] Gegenbaur, Elements of Comparative Anatomy, transl. by F. J. Bell, 1878, p. 515, Gaskell, Journal of Physiology, Vol. x., 1889, p. 153.

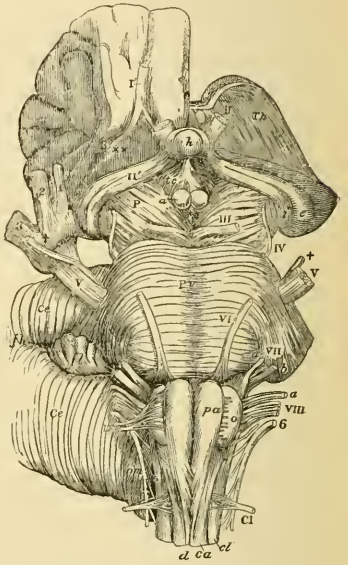
remaining ten pairs, however, while apparently arising like the first two pairs from the base of the brain, in reality originate, as already mentioned, from nuclei in the medulla (Fig. 337), hence our reference to them as medullary nerves. Taking them in the order in which they succeed the olfactory and optic nerves, they are as follows (Figs. 338, 339): The third pair, or motor oculi communis; fourth pair, or patheticus; fifth pair, or trigeminal or

Fig. 337.



View of the posterior surface of the medulla, the roof of the fourth ventricle being removed to show the rhomboid sinus clearly. The left half of the figure represents: *Cu.* Funiculus cuneatus, and *g*, funiculus gracilis. *O.* Obex. *sp.* Nucleus of the spinal accessory. *p.* Nucleus of pneumogastric. *p + sp.* Ala cinera. *R.* Restiform body. *XII'.* Nucleus of the hypoglossal. *t.* Funiculus teres. *a.* Nucleus of the acousticus. *m.* Striæ medullares. 1, 2 and 3. Middle, superior, and inferior cerebellar peduncles respectively. *f.* Fovea anterior. 4. Eminentia teres (genu nervi facialis). 5. Locus cæruleus. The right half of the figure represents the nerve nuclei diagrammatically: *V.* Motor trigeminal nucleus. *V'.* Median and *V''*, inferior sensory and trigeminal nuclei. *VI.* Nucleus of abducens. *VII.* Facial nucleus. *VIII.* Posterior median acoustic nucleus. *VIII'.* Anterior median. *VIII''.* Posterior lateral. *VIII'''.* Anterior lateral acoustic nuclei. *IX.* Glosso-pharyngeal nucleus. *X, XI,* and *XII.* Nuclei of vagus, spinal accessory, and hypo-glossal nerves respectively. The Roman numerals at the side of the figure, from *I* to *XII*, represent the corresponding nerve roots. (Erb.)

Fig. 338.



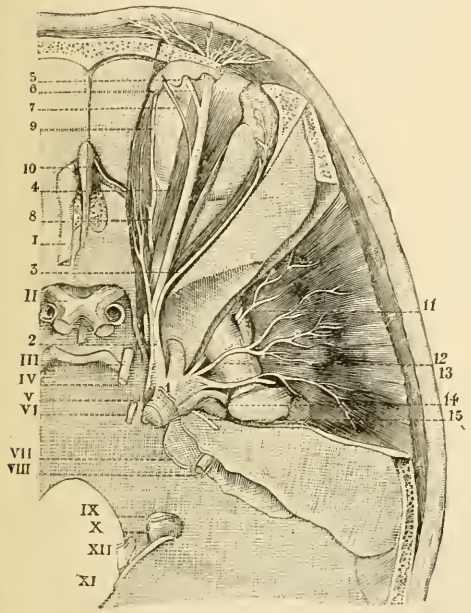
View from below of the connection of the principal nerves with the brain. *I'.* The right olfactory tract. II. The left optic nerve. *II'.* The right optic tract; the left tract is seen passing back into *i* and *e*, the internal and external corpora geniculata. III. The left oculomotor nerve. IV. The trochlear. V, V. The large roots of the trifacial nerves. + +. The lesser roots, the + of the right side is placed on the Gasserian ganglion. 1, the ophthalmic; 2, the superior maxillary; and 3, the inferior maxillary nerves. VI. The left abducent nerve. VII, *a*, *b*. The facial and auditory nerves. *a*, VIII, *b*. The glosso-pharyngeal, pneumogastric, and spinal accessory nerves. IX. The right hypo-glossal nerve. C 1. The left suboccipital or first cervical nerve.

trifacial; sixth pair, or abducens; seventh pair, or facial; eighth pair, or auditory, the special nerve of the sense of hearing; ninth pair, glosso-pharyngeal; tenth pair, pneumogastric; eleventh pair, spinal accessory; twelfth pair, hypo-glossal. The third nerve, or motor oculi communis (Figs. 338 and 339, III), consisting of about 15,000 fibers,[1] arises from a series of nuclei (Fig. 340) situated

[1] Rosenthal, De Numero atque Mensura Microscop Fibrillarum. Breslau, 1845.

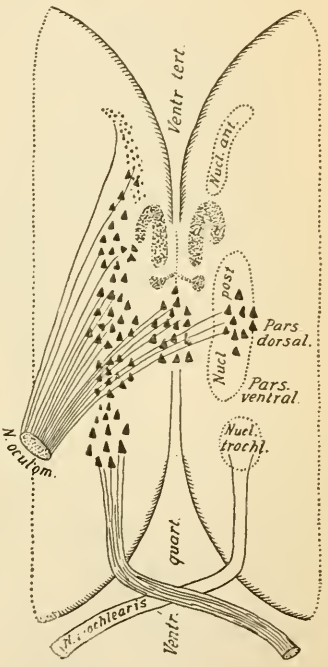
upon both sides of the middle line of the aqueduct of Sylvius beneath the corpora quadrigemina, those of the fibers crossing the middle line decussating with those of the opposite side. The nuclei of the third nerve, and those of the fourth and sixth as well, it may be here mentioned, to avoid repetition, are in rela-

FIG. 339.



Roots of the cranial nerves. I. First pair; olfactory. II. Second pair; optic. III. Third pair; motor oculi communis. IV. Fourth pair; patheticus. V. Fifth pair; nerve of mastication and trifacial. VI. Sixth pair; motor oculi externus. VII. Facial. VIII. Auditory—Seventh pair. IX. Glosso-pharyngeal. X. Pneumogastric. XI. Spinal accessory—Eighth pair. XII. Ninth pair; sublingual. The numbers 1 to 15 refer to branches which will be described hereafter. (HIRSCHFELD.)

FIG. 340.



A partly diagrammatic view of the floor of the aqueduct, looking upward (dorsally), nuclei of the third and fourth nerves, and the decussating fibers of the latter all shown; the third nerve nuclei are subdivided into an anterior nucleus, the Edinger-Westphal nucleus (*a* and *b*), and a posterior nucleus; the posterior nucleus has a dorsal, a ventral, and a mesal portion; the decussation of the fibers from the dorsal portion of the posterior nucleus of the third nerve is shown. (EDINGER.)

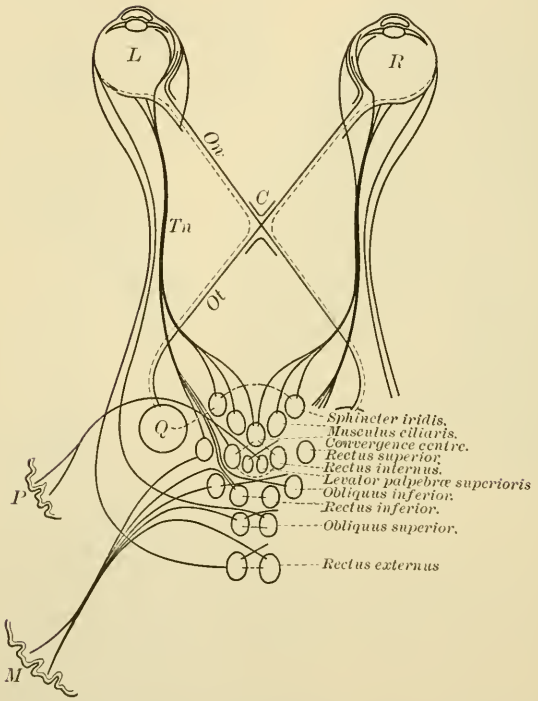
tion, functionally on the one hand with axis-cylinders, which arising in the cells of the motor or visual cortex, descend about the knee of the internal capsule, and on the other by the axis-cylinders, which they give rise to, with the tissues supplied by the ocular nerves.

While some difference of opinion still prevails as regards the relative position occupied by the nuclei giving origin to the different fibers of the third nerve, recent researches[1] render it probable that they are situated from before backwards somewhat in the following order (Fig. 341):

[1] C. K. Mills, The Nervous System and its Diseases, 1898, p. 808.

Sphincter iridis,
Musculus ciliaris,
Convergence center,
Rectus superior,
Rectus internus,
Levator palpebræ superioris,
Obliquus inferior,
Rectus inferior,
Obliquus superior,
Rectus externus.

FIG. 341.

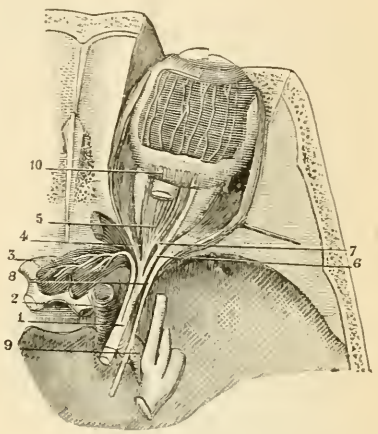


Schema of the nuclei of the nerves of ocular movement and of their central and peripheral tracts. *R.* Right eye. *L.* Left eye. *C.* Chiasm. *On.* Optic nerve. *Ot.* Optic tract. *Q.* Pregeminum (anterior quadrigeminal body). *P.* Cortical center for the movement of elevation of the upper eyelid. *M.* Cortical center for ocular movements. *Tu.* Course of all the ocular nerves in the cavernous sinus. The names of the different nuclei are printed on the diagram, and the nerve tracts going from these nuclei can be readily traced to where they converge in their course in the cavernous sinus and where they diverge to pass to the various muscles of the eye. The dotted line represents associating and commissural tracts. (MILLS.)

From this nucleus the fibers pass forward through the crus, emerging at the base of the brain from the inner surface of the crura cerebri immediately in front of the pons. As the nerve passes through the sphenoidal fissure into the orbit (Fig. 342) it divides into two branches, the superior and smaller branches supplying the superior rectus and levator palpebræ superioris muscles, the inferior and larger branch the internal and inferior recti and

the superior oblique muscles. The latter or inferior branch gives off also a short, thick filament, which passing into the ophthalmic ganglion of the sympathetic is supposed, as we shall see, to pass thence as the short ciliary nerves into the iris, innervating the circular muscular fibers of the latter. During its course the fibers of the third pair run in common or in juxtaposition with fibers derived from the ophthalmic division of the fifth pair, and from the cavernous plexus of the sympathetic. We make use of the expression running in company with, or in juxtaposition with, in preference to that of anastomosis, etc., since the various medullary nerves do not actually receive fibers from or anastomose with each other in the sense that arteries and veins anastomose. The nerves, in fact, never lose their individuality, but undoubtedly preserve through the whole extent of their course the characteristic functions obtaining at their roots, as in the case of the spinal nerves.

FIG. 342.



Distribution of the motor oculi communis. 1. Trunk of the motor oculi communis. 2. Superior branch. 3. Filaments which this branch sends to the superior rectus and the levator palpebræ superioris. 4. Branch to the internal rectus. 5. Branch to the inferior rectus. 6. Branch to the inferior oblique muscle. 7. Branch to the lenticular ganglion. 8. Motor oculi externus. 9. Filaments of the motor oculi externus anastomosing with the sympathetic. 10. Ciliary nerves. (HIRSCHFELD.)

This distinction must be continually borne in mind, for, as we shall see presently, while each of these nerves, at its origin, has a definite function—motor, or sensory—they become, sooner or later, apparently mixed nerves, from the fact of being accompanied by the fibers of the adjacent cranio-medullary nerves. It is in this sense that the third nerve is to be understood as being a motor nerve, any evidences of sensibility being due, not to its intrinsic fibers, but to the extrinsic ones of the fifth pair. That the third nerve is exclusively a motor nerve is shown by the fact of irritation of the root causing contractions of the muscles to which it is distributed, but no pain, while division of the nerve is followed by paralysis of the same.[1] Pathological facts, like the falling of the upper eyelid, or blepharoptosis, external strabismus, immobility of the eye, except outwardly; inability to rotate the eye on its antero-posterior axis in certain directions; slight protrusion of the eyeball; dilation of the pupil, with some interference with the movements of the iris, following disease of the third pair in man, are

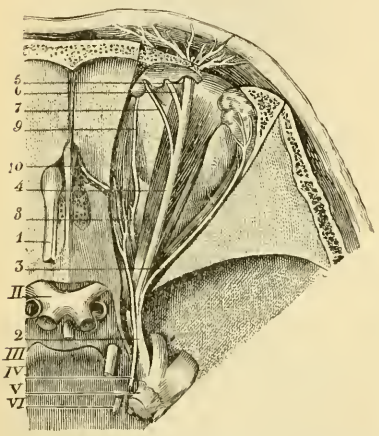
[1] Mayo, Anatomical and Physiological Commentaries, p. 5. London, 1823. Outlines of Human Physiology, p. 294. London, 1827. Bernard, Systeme nerveux, Tome ii., p. 204. Paris, 1858. Chauveau, Journal de physiologie, Tome v., p. 274. Paris, 1862. Longet, Physiologie, Tome iii., p. 554. Paris, 1869.

among the proofs that may be offered that the third pair of nerves is in man motor, as we would be led to suppose it would be, both from its anatomical distribution as well as from the results obtained by vivisection.

The Fourth Nerve.

The fourth nerve, or patheticus, consisting of about 1200 fibers, arises from a nucleus situated immediately posterior to the nucleus of the third nerve (Fig. 340) and gives origin to the fibers supplying the rectus inferior muscle. The fibers so originating cross the middle line of the fourth ventricle and, decussating with those of the opposite side, emerge from the valve of Vieusseus at the base of the brain (Figs. 338 and 339, IV), as comparatively slender filaments at the sides of the pons, and, winding around the crura, pass through the sphenoidal fissure (Fig. 343) into the orbit, and supply the superior oblique muscle. Irritation of the nerve in a living animal, at its origin, causes contraction of the superior oblique muscle, and division of the nerve paralysis of the same.[1] In cases where the nerve is diseased in man, paralysis of the superior oblique muscle is observed as well as immobility of the eyeball, so far as rotation is concerned, and, when the eye is moved toward the shoulder, we have double vision, the eye not rotating to maintain the globe in the same relative position. The pathological facts observed in man, as well as the anatomical distribution, confirm the view based upon vivisections, that the fourth nerve is exclusively motor at its origin, any sensibility it may possess further on in its course being due to adjacent filaments from the ophthalmic branches of the fifth pair, or the sympathetic.

Fig. 343.



Distribution of the patheticus. *I.* Olfactory nerve. *II.* Optic nerves. *III.* Motor oculi communis. *IV.* Patheticus, by the side of the ophthalmic branch of the fifth, and passing to the superior oblique muscle. *VI.* Motor oculi externus. 1. Ganglion of Gasser. 2, 3, 4, 5, 6, 7, 8, 9, 10. Ophthalmic division of the fifth nerve, with its branches. (Hirschfeld.)

The Sixth Nerve.

The sixth nerve, the abducens, or motor oculi externus, being, like the fourth nerve, distributed to a single muscle, the external rectus, and, therefore, exclusively motor in function, will be considered now, before the fifth nerve, which would, otherwise, be the next in order. The sixth nerve, consisting of about 3000 fibers, arises from a nucleus, situated beneath the eminentia teres, in the middle of the floor of the fourth ventricle (Fig. 337, *VI*) just pos-

[1] Longet, op. cit., Tome iii., p. 557. Chauveau, op. cit., Tome v., p. 275.

terior to the nucleus, giving origin to the fourth nerve. Unlike the fibers of the third and fourth pairs, it has not yet been shown that the fibers of the sixth nerve decussate at their origin in the floor of the fourth ventricle. The sixth nerve appears at the base of the brain in the groove separating the anterior pyramid of the medulla from the pons (Fig. 338), and passes thence through the sphenoidal fissure into the orbit. While in its course the sixth nerve runs in juxtaposition with the filaments derived from the sensitive ophthalmic branch of the fifth pair, and from the sympathetic through the carotid plexus, and Meckel's ganglion. It is undoubtedly exclusively a motor nerve, supplying only the external rectus muscle (Fig. 342, 8). Irritation of the nerve at the root in a living animal causes the latter muscle to contract, but no pain, while division of the nerve is followed by paralysis of the external rectus and internal strabismus,[1] the latter being also observed in man in cases of disease of the sixth nerve. The third, fourth, and sixth pairs of nerves, taken together, constitute the efferent or motor nerves in the reflex actions involved in the movements of the pupil and the eyeball in vision, and which will be considered hereafter, the optic nerve and the ophthalmic division of the fifth nerve constituting the afferent or sensory nerves.

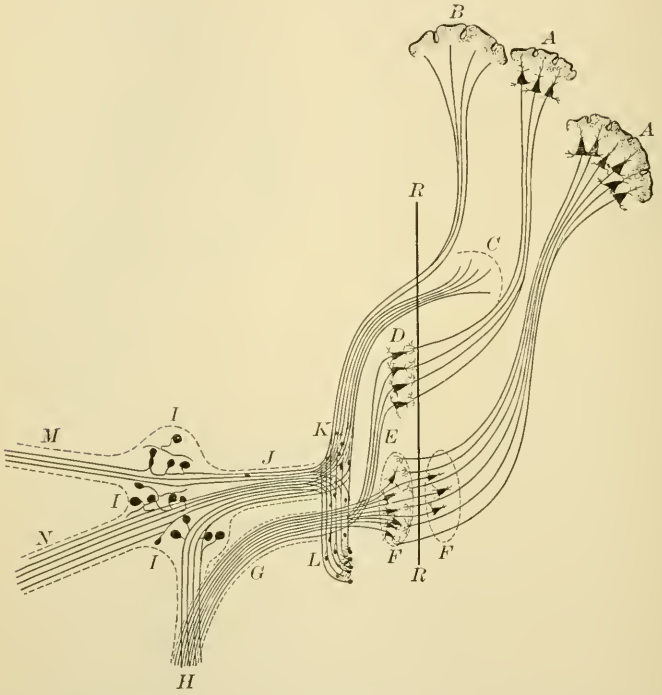
The Fifth Nerve.

The fifth nerve, trifacial, or trigeminus, in arising from the base of the brain by two roots (Fig. 338, V +), the posterior large and sensory, with ganglion attached, and the anterior small and motor, is usually regarded as especially comparable with a spinal nerve. For the reasons already given, it is quite as possible, however, that the fibers of the third, fourth, and even of the sixth nerves may constitute the true motor fibers corresponding to the sensory fibers of the fifth (ophthalmic and superior maxillary) as that the fibers of its small motor root should be so especially regarded, particularly as the latter, as we shall see presently, are distributed exclusively in company with the fibers of the inferior maxillary branch of the fifth. Of the two roots of which the fifth nerve consists (Fig. 344, *J*, *G*), the larger or sensory root appears, from recent researches,[2] to arise in the Gasserian or semilunar ganglion, situated in the depression on the internal portion of the anterior face of the petrous portion of the temporal bone rather than to pass into it, as usually stated. The axis-cylinders of the cells of the ganglion divide into two branches, of which one set pass towards the brain, decussating with the fibers of the opposite side, as the long root (*J*), the other set peripherally as the ophthalmic (*M*), the superior maxillary (*N*), and the inferior maxillary (*H*) nerves. Of the 30,000 fibers passing as the long root (*J*) towards the brain, some ascending cross the middle line and terminate in the thalamus opticus (*C*) and sensory areas of the cortex (*B*) of the opposite hemisphere, others descending (*L*) pass into the cervical region of the spinal cord. The

[1] Longet, op. cit., Tome iii., p. 560. Chauveau, op. cit., Tome v., p. 275.
[2] S. Ramón y Cayal, Beitrag Zum Studium Der Medulla Oblongata, 1896, s. 1.

fibers of the small or motor root (*G*) arise from the cells of two centers, a chief motor center (*F*) situated in the floor of the fourth ventricle and an accessory motor one (*D*) beneath the corpora quadrigemina, and which are in relation with the cells of the cortex (*A*, *A*) of the lower part of the central convolutions of the opposite hemisphere and decussating with those of the opposite side. The two sets of fibers so arising pass together peripherally (*G*), and, running juxtaposed with the most inferior of the sensory fibers of the long root, constitute the inferior maxillary nerve (*H*). The an-

FIG. 344.



Schema of trigeminal apparatus. *A A*. Cortical centers for trigeminal motor tracts. *B*. Cortical terminus of the trigeminal sensory tract. *C*. Thalamus to which the central trigeminal sensory tract may be in large part distributed. *D*. Accessory (motor) nucleus. *E*. Descending (mesencephalic) root. *F*. Chief motor nucleus. *G*. Motor roots. *H*. Inferior maxillary nerve. *I*. Gasserian ganglion. *J*. Sensory roots between the Gasserian ganglion and the pons. *K*. Ascending sensory root. *L*. Descending (spinal) root. *M*. First or ophthalmic division of the trigeminus. *N*. Second or superior maxillary division. (MILLS.)

terior small or motor root, consisting of about 10,000 fibers, passes underneath the ganglion of Gasser, from which it occasionally receives a few filaments, and lying behind the inferior maxillary branch of the large root, passes through the foramen ovale in company with the latter, with which it is finally distributed. It will be observed that while the ophthalmic and superior maxillary branches of the fifth are purely sensory, being derived solely from the large root through the Gasserian ganglion, the inferior maxillary branch is both motor and sensory, being derived not only from the ganglion but from the small or motor root as well.

In division of the nerve in a living animal with the view of determining its function [1] both roots are necessarily divided, and with the complete loss of sensibility ensuing under such circumstances, there is also observed paralysis of the temporal, masseter, internal and external pterygoid, mylo-hyoid, and anterior belly of the digastric muscles, or the muscles of mastication supplied by the fibers of the small root running in the inferior maxillary division of the fifth nerve and of the tensor muscles of the velum palati, and probably of the tensor tympani also. The effect of division of the fifth nerve is very striking in the case of the rabbit, in which, through the consequent paralysis of the muscles of mastication, the line of contact between the incisor teeth becomes oblique instead of horizontal, the incisor teeth being worn away unevenly through the jaw being drawn to one side by the action of the active muscles.

While it is an extremely difficult operation, if not impossible, to stimulate the small root of the fifth nerve in a living animal, nevertheless, there can be little doubt that it is a purely motor nerve in function, since if it be stimulated in an animal just dead, in which the cerebral lobes have been removed, such of the muscles of mastication as are supplied by the nerves of the small root (running in the inferior maxillary division of the fifth) at once contract,[2] and in the case of old horses, for example, with such force as to break off pieces of the teeth,[3] no such result following stimulation of the large root.

The cases of paralysis of the fifth nerve that have been noted in man confirm in the main the results of experiments made upon animals. In all instances where both the large and small roots were involved by the disease, entire loss of sensibility and paralysis of the muscles supplied by the fifth were observed [4] the only cases in which there was no paralysis of the muscles of mastication, etc., being those in which the small root was unaffected, loss of sensibility on the side affected being then only noted.

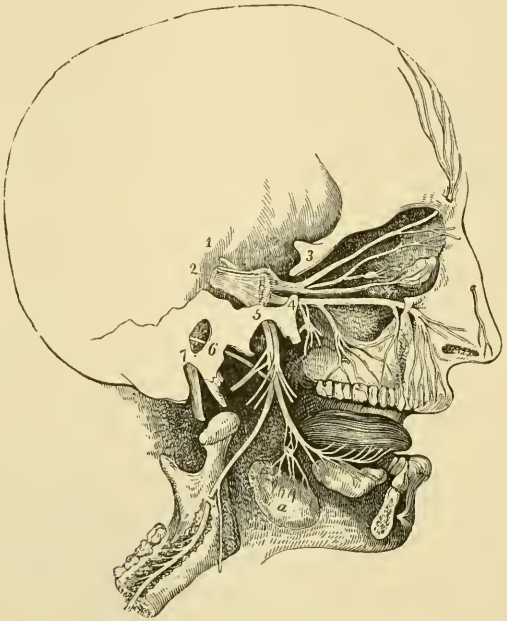
In order to appreciate the results following division of the large root of the fifth nerve in a living animal or disease in man, it will be first necessary to describe briefly the distribution of its principal branches. It has already been mentioned that the large root arising in the ganglion of Gasser passes thence peripherally as the ophthalmic superior and inferior maxillary nerves.

The ophthalmic, the smallest of the three branches of the large root (Fig. 345, below 3), passes through the sphenoidal fissure into the orbit, subdividing into the lachrymal, frontal, and nasal nerves, and gives off during its course to the orbit, fibers to the third, fourth, and sixth nerves, to the tentorium and to the sympathetic. The lachrymal nerve supplies the lachrymal gland, conjunctiva, integument of the upper eyelid, and gives off fibers to the orbital branch of the superior maxillary. The frontal

[1] Bernard, Systeme nerveux, Tome ii., p. 100. Paris, 1858.
[2] Longet, Anat. et Phys. du systeme nerveux, Tome ii., p. 190. Paris, 1842.
[3] Chauveau, op. cit., p. 276.
[4] Langet, op. cit., p. 191; Mills, op. cit., pp. 890–895.

branch divides into the supratrochlear and supraorbital nerves, the former nerve supplies the integument of the forehead and gives off a long, delicate filament to the nasal nerve; the latter, or supraorbital nerve, passing through the supraorbital foramen, supplies, to a certain extent, the upper eyelid and forehead, the anterior and median portions of the scalp, the mucous membrane of the frontal sinus, and the pericranium covering the frontal and parietal bones.

Fig. 345.

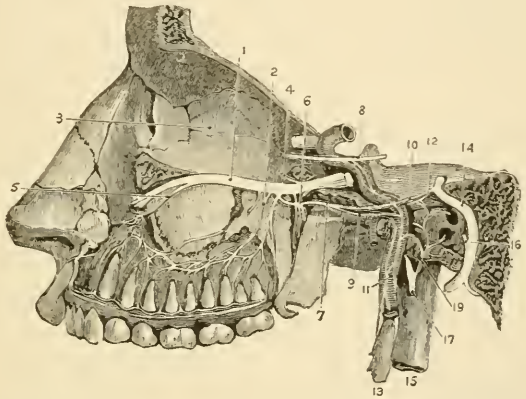


General plan of the branches of the fifth pair. 1. Lesser root of the fifth pair. 2. Greater root passing forward into the Gasserian ganglion. 3. Placed on the bone above the ophthalmic nerve, which is seen dividing into the supraorbital, lachrymal, and nasal branches, the latter connected with the ophthalmic ganglion. 4. Placed on the bone close to the foramen rotundum, marks the superior maxillary division. 5. Placed on the bone over the foramen ovale, marks the submaxillary nerve. (After a sketch by Charles Bell.) ⅓.

The nasal branch, before entering the orbit, gives off a long filament to the ophthalmic ganglion, and then the long ciliary nerves supplying the ciliary muscle, iris, and cornea; it then divides into the external nasal, or infra-trochlearis, and the internal nasal, or ethmoidal nerves. The infra-trochlearis nerve supplies the integument of the forehead and nose, the internal surface of the lower eyelid, the lachrymal sac, and caruncula. The internal nasal, or ethmoidal nerve, supplies the mucous membrane of the nose, and partly its integument. The second branch of the fifth nerve, the superior maxillary nerve (Fig. 346, 1), passes out of the cranium by the foramen rotundum, and traversing the infraorbital canal emerges by the infraorbital foramen upon the face, giving off palpebral branches to the lower eyelid, nasal branches to the side of the nose, the latter running in common with the nasal branch of the ophthal-

mic and labial branches to the integument and mucous membrane of the upper lip. During its course through the spheno-maxillary fossa the superior maxillary nerve gives off several branches; the orbital, which, passing into the orbit, gives off, in turn, the temporal and malar nerves, which, emerging by foramina in the malar bones, are distributed to the integument of the temple and side of the forehead, and the integument covering the malar bone respectively, the two posterior dental nerves (Fig. 346), the latter supplying the

FIG. 346.



Dissection of the superior maxillary nerve and Meckel's ganglion. 1. Superior maxillary nerve. 2. Posterior dental nerves. 3. Inner wall of orbit. 4. Orbital branch (cut). 5. Anterior dental nerve. 6. Meckel's ganglion. 7. Vidian nerve. 8. Sixth nerve. 9. Carotid branch of Vidian. 10. Greater superficial petrosal nerve. 11. Carotid plexus of sympathetic. 12. Lesser superficial petrosal nerve. 13. Superior cervical ganglion of sympathetic. 14. Facial nerve. 15. Internal jugular vein. 16. Chorda tympani nerve. 17. Glosso-pharyngeal nerve. 19. Jacobson's nerve. (From HIRSCHFELD and LEVEILLÉ.)

molar and bicuspid teeth, the mucous membrane of the alveolar processes and of the antrum. In the infraorbital canal the anterior dental is given off, constituting, together with the posterior dental, the dental arcade, the anterior dental supplying the canine and incisor teeth, and the mucous membrane of the alveolar processes. The third branch of the fifth nerve, or the inferior maxillary (Fig. 345, 5), passes out of the cranial cavity by the foramen ovale, and after uniting with the small or motor root of the fifth, divides into anterior and posterior branches, the anterior branch containing the motor fibers supplying the principal muscles of mastication, and the tensor muscles of the velum palati through the otic ganglion, and derived, as already mentioned, from the small or motor root, the posterior branch containing principally sensory fibers. Among the most important of these may be mentioned the auriculo-temporal, the lingual, and the inferior dental nerves. The auriculo-temporal nerve supplies the integument of the temporal region of the ear, the auditory meatus, the temporo-maxillary articulation, and the parotid gland; it gives off, also, filaments that run in common with those of the seventh nerve, or facial. The lingual nerve, distributed to the mucous membrane of the point of the tongue, mouth, gums, sub-

lingual gland, submaxillary ganglion, consists, as we shall see, through a considerable extent of its course, of two distinct nerves, the lingual proper and the chorda tympani, and whose relations will be considered presently. The inferior dental nerve, after giving off the mylo-hyoid nerve, passes through the dental canal in the inferior maxillary bone, and supplying the lower teeth, emerges upon the face at the mental foramen, and, as the mental nerve, supplies the integument of the chin, the lower part of the face, and lower lip, and partly the mucous membrane of the mouth. While, as already mentioned, it is impossible to stimulate directly the large root of the fifth nerve in a living animal, yet, since all of its accessible branches, both in man and animals, have been shown to be very sensitive, it might reasonably be inferred that the large root from which all these branches arise is sensory in function, especially when it is remembered that its stimulation in an animal just dead is followed by no contractions of the muscles to which the fifth nerve is distributed. Further, as well known,[1] if the large root be divided in a living animal, entire loss of sensibility on the side of the head affected at once follows, any muscular paralysis ensuing being limited to the parts supplied by the fibers of the small or motor root. The immediate effect of division of the large root is very striking, the cornea, integument, and mucous membrane of the side affected are at once deprived of sensibility, and may be burned, lacerated, or pricked without the animal evincing any pain. Loss of general sensibility in the tongue is also observed, though no loss of taste,[2] since, as we shall see hereafter, the gustatory properties of the anterior part of the tongue are due to the chorda tympanic fibers of the lingual nerve, and not to those fibers of the lingual proper derived from the inferior maxillary branch of the fifth nerve.

The loss of general sensibility, etc., are also observed in paralysis of the fifth nerve occurring in human beings. In one of these cases,[3] it may be mentioned as a proof of the sensory properties of the large root of the fifth nerve, that an operation was performed without the slightest evidence of pain on the part of the patient. In addition to the loss of sensibility, etc., following division of the large root of the fifth nerve, in certain cases inflammation of the eye, ear, and nose have also been observed, the eye on the side affected becoming the seat of purulent inflammation; the cornea, after becoming opaque, ulcerating, the humors of the eye discharging, and the organ destroyed. Ulcers also appear upon the tongue and lips, and there is a discharge from the mucous membrane of the nose and mouth, and the hearing appears to be affected. The impairment in the nutrition of the eye, mouth, etc., following division of the fifth nerve, appears to be due rather to inflammatory irritation

[1] Magendie, Journal de Physiologie, Tome iv., pp. 176, 302. Paris, 1824. Bernard, Leçons sur la physiologie et la pathologie du Systeme nerveux, Tome ii., p. 53. Paris, 1858.

[2] Schiff, Leçons sur la physiologie de la digestion, Tome i., p. 103. Florence, 1867. Lusanna, Archives de Phys., Tome ii., p. 27. Paris, 1869.

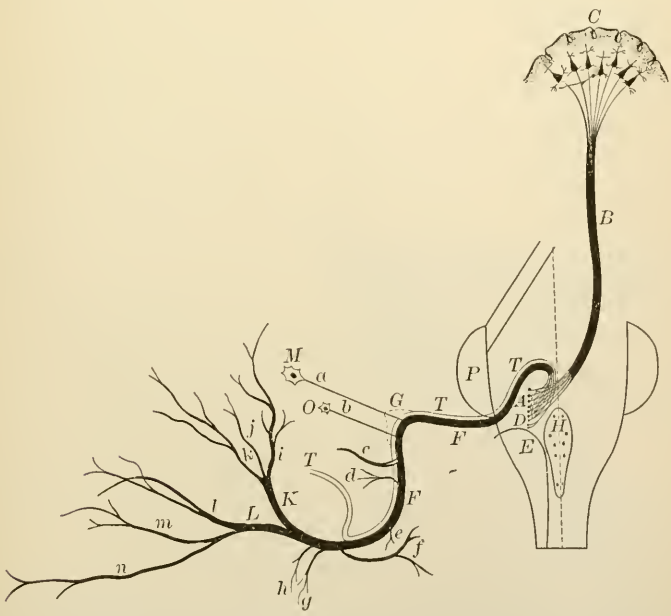
[3] Noyes, New York Med. Journal, 1871, Vol. xiv., p. 163.

of the nerve than to division of the fibers of the sympathetic passing into the Gasserian ganglion with consequent vasomotor disturbance as was formerly supposed. That the paralysis of the muscles of mastication incidental to the division of the fifth nerve which interferes seriously with the digestion of food may account to some extent for the disturbances of nutrition just mentioned appears to be shown from the fact that the inflammation of the eye, etc., can be prevented, for some weeks at least, if the animal be artificially fed with good nutritive food. It need hardly be mentioned that the nervous fibers transmitting gustatory, olfactory, and auditory impressions are not in any way derived from the large root of the fifth nerve, as once thought, the large root being only a nerve of general sensibility, the small root of motion.

The Seventh Nerve.

The seventh nerve, the nerve of expression, the facial, or the portio dura of the seventh pair, supposing the latter to include, as in the arrangement of Willis, not only the fibers of the facial proper, but those of the auditory, or porto mollis, containing about 4,500 fibers, arises in a fan-shaped manner from a group of cells situated in the gray matter of the floor of the fourth ventricle (Figs. 337, *VII;* 347, *A*).

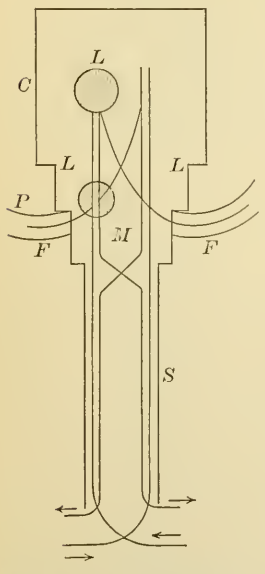
FIG. 347.



Schema of the apparatus of the facial nerve. *P.* Pons. *A.* Facial nucleus. *B.* Facial cortico-bulbar tract. *C.* Cortical center for facial movements. *D.* Nucleus of the pars intermedia of Wrisberg. *E.* Descending glosso-pharyngeal roots. *H.* Nucleus of the hypo-glossal nerve. *FF.* Trunk of the facial nerve. *G.* Geniculate ganglion. *TTT.* Pars intermedia of Wrisberg and chorda tympani nerve. *M.* Meckel's spheno-palatine ganglion. *O.* Otic ganglion. *a.* Great superficial petrosal and Vidian nerves. *b.* Lesser superficial petrosal nerve. *c.* External superficial petrosal nerve; branch of the facial nerve to the stapedius muscle. *e.* Branch of the facial to the auricular branch of the vagus. *f.* Posterior auricular branch. *g.* Digastric branch. *h.* Stylo-hyoid branch. *i.* Temporal branch. *j.* Malar branch. *k.* Infraorbital branch. *l.* Buccal branch. *m.* Supramaxillary branch. *n.* Inframaxillary branch. (MILLS.)

The fibers so arising pass from the floor of the fourth ventricle as a compact bundle which, curving over the nucleus of the sixth nerve horseshoe like (Fig. 347, *T*), turns obliquely outward and emerges, together with the pars intermedia or nerve of Wrisberg, from the transverse fibers of the pons *P* between the abducens and acoustic nerves. The facial nucleus is in relation with axis-cylinders which, crossing the middle line of the floor of the fourth ventricle and decussating with the fibers of the opposite nerve, pass through the knee of the internal capsule, and the corona radiata into the motor cells of the lower extremity of the central convolution *C* of the opposite hemisphere. According to some observers the facial nucleus is also connected by axis-cylinders from the substantia gelatinosa of the cord with the descending spinal root of the fifth nerve. That the fibers of the facial nerve decussate in the pons as just described is shown by the fact of what is known as "alternate paralysis," it being well known that if a lesion be situated in the pons, Fig. 348, *L*, the facial paralysis and that of motion and sensation will be on opposite sides of the body, whereas if the lesions be situated anterior to the pons, the facial paralysis and that of motion and sensation will be on the same side of the body.

Fig. 348.



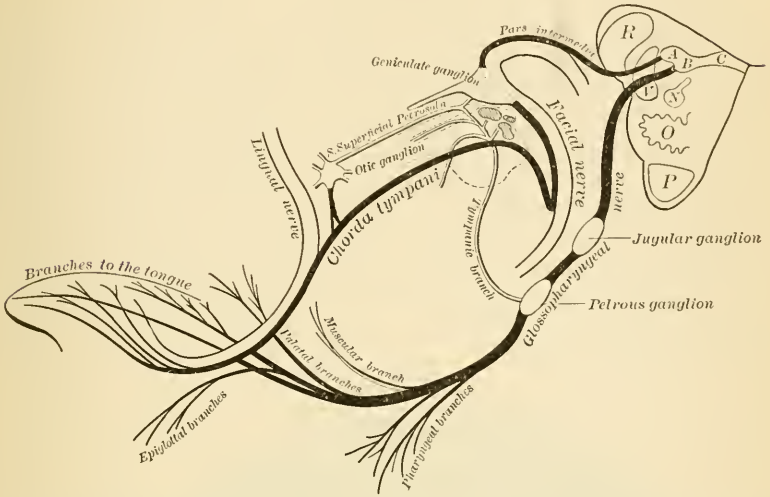
To illustrate alternate paralysis. *C.* Cerebrum. *P.* Pons. *M.* Medulla. *F.* Facial. *L.* Lesion. *S.* Spinal cord.

The facial, pars intermedia, and auditory nerves, after leaving the base of the brain, pass thence into the internal auditory meatus, the pars intermedia being connected in this part of its course with the auditory nerve, a relation the functional significance of which it may be stated has not yet been shown. Leaving for the present the further consideration of the auditory nerve, the facial and the pars intermedia will be found to enter the Fallopian canal, the pars intermedia presenting a gangliform enlargement, the geniculate ganglion, and passing by this route through the petrous portion of the temporal bone the two nerves unite and emerge as a common trunk by the stylo-mastoid foramen.

Considerable difference of opinion still prevails as to the exact origin and distribution of the pars intermedia which we have just seen emerges from the base of the brain between the facial and auditory nerves. According to recent observations the pars intermedia, regarded by some histologists as a root or branch of the facial, by others as a distinct nerve, arises or rather terminates in the nucleus of the glosso-pharyngeal nerve (Fig. 349, *A*) from the cells of which fibers run for a time juxtaposed with those of the facial proper and thence pass peripherally as the chorda by

certain nerves. On the other hand, there are good reasons, as we shall see presently, for supposing that the chorda tympani nerve

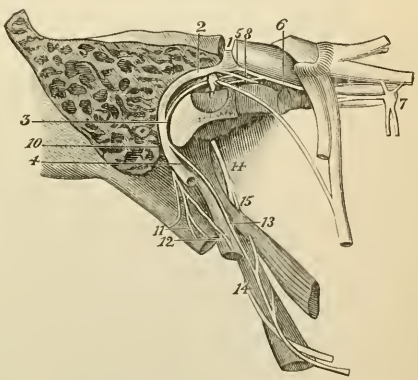
FIG. 349.



Peripheral gustatory apparatus. *A*. Portion of the sensory glosso-pharyngeal nucleus in which the pars intermedia terminates. *B*. Main portion of the sensory glosso-pharyngeal nucleus. *C*. Commissural nucleus of Ramón y Cajal. *N*. Nucleus ambiguus. *O*. Olive. *P*. Pyramid. *R*. Restis. *V*. Spinal root of the fifth nerve. (MILLS.)

is the continuation of the great petrosal nerve, the two nerves being connected in the geniculate ganglia. The significance of these relations will be better appreciated, however, when the peripheral distribution of the facial has been described.

FIG. 350.

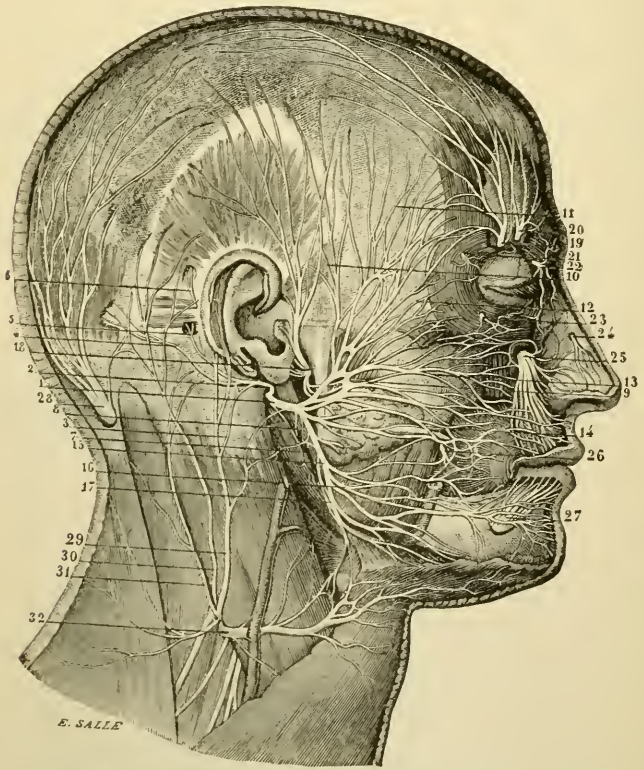


1, 2, 3, 4. Facial nerve passing through the aquæductus Fallopii. 5. Gangliform enlargement. 6. Great petrosal nerve. 7. Spheno-palatine ganglion. 8. Small petrosal nerve. 9. Chorda tympani. 10, 11, 12, 13. Various branches of the facial. 14, 14, 15. Glosso-pharyngeal nerve. (HIRSCHFELD.)

The most important branches of the facial are briefly as follows: The large and small petrosal nerves passing, respectively, to Meckel's and the otic ganglia (Fig. 349), the external petrosal to the sympathetic fibers of the middle meningeal artery, the tympanic branch distributed to the stapedius muscle, the chorda tympani nerve (Figs. 349, 350) passing through the tympanum to join the lingual branch of the inferior maxillary, the branch to the pneumogastric.

The six branches just mentioned are given off by the facial during its course through the aqueduct of Fallopius. The remaining branches still to be mentioned are given off after the nerve has emerged from the stylo-mastoid foramen, the branch to the glosso-pharyngeal nerve, the posterior auricular connected with the cervical plexus by the auricularis magnus and distributed to the retrahens and attolens aurem, the occipital portion of the occipito-frontalis muscle, and the integument, the digastric branch receiving filaments from the glosso-pharyngeal supplying the posterior belly of the muscle of the same name and the stylo-hyoid, a distinct branch also to the stylo-hyoid muscle, the lingual branch—that is, the branch passing behind the stylo-pharyngeus muscle and receiving filaments from the glosso-pharyngeal nerve to be distributed to the mucous membrane, tongue, stylo-glossus, and palato-glossus muscles, and finally, the temporo-facial and cervico-facial branches (Fig. 351) into which the main trunk divides as it passes through the parotid gland.

FIG. 351.



Superficial branches of the facial and the fifth. 1. Trunk of the facial. 2. Posterior auricular nerve. 3. Branch which it receives from the cervical plexus. 4. Occipital branch. 5, 6. Branches to the muscles of the ear. 7. Digastric branches. 8. Branch to the stylo-hyoid muscle. 9. Superior terminal branch. 10. Temporal branches. 11. Frontal branches. 12. Branches to the orbicularis palpebrarum. 13. Nasal, or suborbital branches. 14. Buccal branches. 15. Inferior terminal branch. 16. Mental branches. 17. Cervical branches. 18. Superficial temporal nerve (branch of the fifth). 19, 20. Frontal nerve (branches of the fifth). 21, 22, 23, 24, 25, 26, 27. Branches of the fifth. 28, 29, 30, 31, 32. Branches of the cervical nerves. (HIRSCHFELD.)

The temporo-facial branch passing upward and forward is distributed to the attrahens aurem, the frontal portion of the occipito-frontalis, the orbicularis palpebrarum, corrugator supercilii, pyramidalis nasi, levator labii superioris, alæque nasi, the dilator and compressor nasi, part of the buccinator, the levator anguli oris, and the zygomatic muscles. During its course the temporo-facial branch receives filaments from the auriculo-temporal branch of the inferior maxillary nerve, from the temporal branch of the superior maxillary, and from the ophthalmic ; it becomes, therefore, a mixed nerve in function. The cervico-facial nerve, passing downward, supplies the buccinator, orbicularis oris, risorius, levator labii inferioris, depressor labii inferioris, depressor anguli oris, and platysma myoides. From the fact that division of the fifth nerve is at once followed by entire loss of sensibility in the parts supplied by that nerve, it is evident that the facial, supplying to a considerable extent identical regions, cannot be a sensory nerve, otherwise sensibility, though weakened, should nevertheless persist in the face, etc., even after division of the fifth nerve. Direct evidence, however, as well as indirect, proves conclusively that the seventh nerve, at its origin at least, is a purely motor nerve. Thus, division of the nerve in a living animal or disease in man is at once followed by paralysis of the facial and other muscles that we have just seen are supplied by the nerve, while stimulation of the nerve at its root in a living animal or in one recently dead, causes contraction of the muscles, but in the case of the living animal no pain. Any sensibility then exhibited by the facial nerve beyond its root must be attributed to the fibers derived from the fifth nerve, glosso-pharyngeal, and pneumogastric, that we have seen run in juxtaposition with it. In order to appreciate the varied and important functions of the facial nerve, it will be best to consider those of its branches seriatim. In the consideration of the sympathetic, to be taken up hereafter, it will be then shown that the nerve fibers supplying the levator palati, azygos uvulæ, palato-pharyngeus, and palato-glossus are derived from the ganglion of Meckel, and those supplying the tensor palati and tensor tympani from the otic ganglion ; and on the supposition that the great and small petrosal nerves pass respectively through the two ganglia to the muscles just mentioned, supplied by the latter, it might be inferred that paralysis of the facial nerve would be accompanied with difficulty in deglutition and an increased sensitiveness to sound, the tympanic membrane being relaxed through the paralysis of the tensor-tympani muscle, it being well known that the tympanic membrane[1] vibrates more intensely when relaxed than when tensed. Clinical cases of facial paralysis occurring in man fully confirm this view, since in such cases both difficulty in deglutition and increased susceptibility to sounds, etc., are observed.[2]

[1] Muller's Elements of Physiology, Vol. ii., p. 1256. London, 1843.

[2] Montant, Dessertation sur l'hemiplegie faciale these 300, Paris 1831. Bell, The Nervous System, London 1844, p. 329. Bernard, Leçons sur la physiologie et la pathologie du systeme nerveux. Paris, 1858, Tome xi., pp. 114, 113. Mills, op. cit. p. 907.

Further, as confirming the view that the muscles of deglutition are supplied by the facial, may be mentioned the fact of the facial nerve giving off the branch already alluded to supplying the stylo-glossus and palato-glossus muscles, and occasionally of the branch distributed to the palato-glossus and palato-pharyngeus muscles passing directly to the latter without being connected with the glosso-pharyngeal, as is usually the case.[1]

It must be mentioned, however, that according to Gowers[2] in more than one hundred cases of facial paralysis due to disease of the nerve in various situations no defect of movement in the palate was ever observed. Such being the case it is obvious that the motor fibers innervating the palate must be derived, in some cases at least, perhaps in all, not only from the facial, but from other nerves as well. From the fact that the motor fibers innervating the tensor palate are derived from the otic ganglion and that in certain cases, at least, of disease of the fifth nerve deglutition is interfered with or rendered impossible, it has been inferred by some physiologists[3] that the motor fibers innervating the tensor palate are derived from these fibers of the small or motor root of the fifth nerve that pass into the otic ganglion. On the other hand, it has been shown that stimulation of the spinal accessory nerve in certain animals causes contractions of the palate,[4] the impulses passing to the latter either by the branch that the pneumogastric gives to the pharyngeal plexus or possibly by the tympanic branch of the glosso-pharyngeal, some of the fibers of which pass to the otic ganglion. Further, it is well known that in disease of the spinal accessory nerve, movement of the palate on the same side is lost.[5] The facts of experiment and clinical medicine render it highly probable, therefore, that the spinal accessory nerve is the motor nerve of the palate. With such discordant views still prevailing it must be admitted that the nerve fibers innervating the muscles of the palate have not yet been positively determined.

The chorda tympani nerve (Fig. 350), one of the most remarkable nerves in the body, both on account of its origin and distribution as well as of its properties, is usually said to arise from the facial in the aqueduct of Fallopius and passing by a special canal into the tympanum crosses the latter cavity between the incus and malleus and emerges by the canal of Hugier to join the lingual nerve at an acute angle.

In the horse and calf, however, as shown by Owen,[6] the chorda tympani nerve (Fig. 352), while apparently arising from the facial, as

[1] Longet, op. cit., Tome iii., p. 581.
[2] Gowers, op. cit., Vol. ii., p. 236.
[3] Mills, op. cit., pp. 890, 895.
[4] W. A. Turner, Journal of Anat. and Phys., 1889. Beaver and Horsley, Proc. Royal Society.
[5] Gowers, op. cit., Vol. ii., p. 307.
[6] The Anatomy of Vertebrates, Vol. iii., p. 156. London, 1868.

in man, in reality can be traced through the fibers of the facial as a continuation of the large petrosal, and as the latter nerve is connected through the ganglion of Meckel with the superior maxillary nerve a pathway evidently exists in these animals by which the impressions made upon the tongue can be transmitted to the latter nerve, and while the chorda tympani nerve has not been actually demonstrated in man to be a continuation of the large petrosal, as in Fig. 352, both experiments upon animals and pathological cases in man lead one, as we shall see, to suppose that such is substantially the case.[1] On the other hand, apart from the fact of nerve fibers not anastomosing, there is direct experimental evidence to show that the chorda tympanic fibers do not lose their individuality after joining those of the lingual branch of the inferior maxillary, but preserve their functional activity entirely independent of those of the latter. Thus, if the lingual branch of the inferior maxillary be divided before it is joined by the chorda tympani, its fibers alone atrophy, with ensuing loss of general sensibility of the anterior part of the tongue, whereas, if the chorda tympani nerve be divided before it reaches the lingual its terminal fibers alone atrophy, loss of taste ensuing.

Fig. 352.

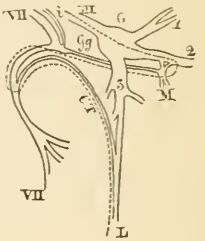


Diagram to illustrate supposed connection of chorda tympani with superior maxillary through facial, great petrosal, and ganglion of Meckel.

Experiment not only shows, however, that the terminal portion of the lingual nerve consists of fibers derived from both the lingual branch of the inferior maxillary, and from the chorda tympani, but that the latter consists of three distinct sets of fibers; 1st, those endowing the anterior two-thirds of the tongue with the sense of taste; 2d, those modifying the blood vessels of the tongue, vasa dilator nerves; 3d, those stimulating through the submaxillary ganglion the submaxillary and sublingual glands. The chorda tympani nerve, consisting, as it undoubtedly does, then, of sensory, motor, and secretory fibers, it is to be expected that it should have specially different centers of origin, which is in harmony with the view just offered of its motor fibers being derived from the facial, and its sensory fibers from the superior maxillary nerve through the large petrosal and the ganglion of Meckel. That the chorda tympani nerve does contain at least some fibers derived from the superior maxillary nerve is further shown from the fact that disease of the fifth nerve, removal of the ganglia of Gasser and Meckel in man, is followed by the loss of the sense of taste in the anterior two-thirds of the tongue.[2] It must be admitted, however, that it

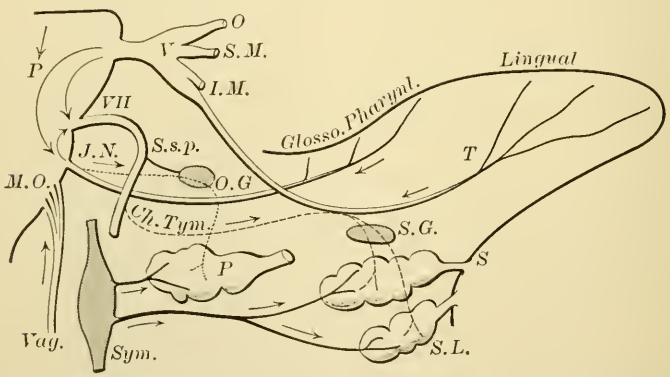
[1] Gowers, op. cit., Vol. ii., p. 214.

[2] Schiff, Leçons sur la Physiologie de Digestion, Tome premier, p. 100. Florence and Turin. Gowers, op. cit., Vol. ii., p. 216. Mills, op. cit., p. 694.

is held by many physiologists at the present day that the chorda tympani ministers to the sense of taste of the supposition that its fibers are continuous with those of the pars intermedia and that the latter nerve is endowed with gustatory properties because derived from the glosso-pharyngeal.[1] The well-known fact that disease of the facial nerve situated between the origin of the chorda tympani and the geniculate ganglion is accompanied with loss of taste in the anterior part of the tongue[2] has been cited as a proof that the chorda tympani is continuous with the great petrosal. It is obvious, however, from what has just been said that the fact of disease of the facial involving the sense of taste might be offered equally well as a proof that the chorda tympani is continuous with the pars intermedia.

It may be mentioned in this connection that, even if the view that the chorda tympani is derived from the pars intermedia is not admitted, the fact that the latter unites with the facial in the Fallopian canal is not without functional significance, since it is well

FIG. 353.



Schema of the nerves of the salivary glands. *P.* Pons. *MO.* Medulla oblongata. *JN.* Nerve of Jacobson. *O, SM, IM.* Ophthalmic, superior, and inferior maxillary divisions of V, fifth nerve. *VII.* Seventh nerve. *Ssp.* Small superficial petrosal nerve. *Vag.* Vagus. *Sym.* Sympathetic. *OG.* Otic, and *SG.* Submaxillary ganglia. *P, S, L.* Parotid, sub-maxillary and sub-lingual glands. *T.* Tongue. (LANDOIS.)

known that the facial, after emerging from the stylo-mastoid foramen, contains sensory fibers, which may account for sensation being more or less restored in certain cases of removal of the Gasserian ganglion. Leaving the further account of the gustatory fibers of the chorda tympani for the present, let us turn now to the consideration of those of its fibers that, passing to the submaxillary ganglion (Fig. 353, *SG*), constitute, together with the sympathetic fibers

[1] Mills, op. cit., p. 686.

[2] Bernard, Systeme Nerveux, 1858, Tome ii., p. 122. Schiff, op. cit., Tome i., p. 183. Lusanna, Archives de Physiologie, Tome ii., p. 201. Paris, 1869. Gowers, op. cit., Vol. ii., p. 237.

accompanying the blood vessels, the efferent fibers involved in the reflex production of saliva by the submaxillary and sublingual glands, the lingual glosso-pharyngeal and pneumogastric nerves, the afferent fibers, the center of the reflex arc being situated in the medulla at the origin of the seventh and ninth cervical nerve. It may be mentioned, in this connection as appropriately as elsewhere, that while in the reflex production of saliva by the parotid gland the afferent nerves are the same as in the case of the submaxillary and sublingual nerves; the efferent nerves involved, in addition to sympathetic fibers, are derived from the otic ganglion, from the facial by the small petrosal, and from the glosso-pharyngeal nerve by the tympani branch of the glosso-pharyngeal or Jacobson's nerve.

FIG. 354.

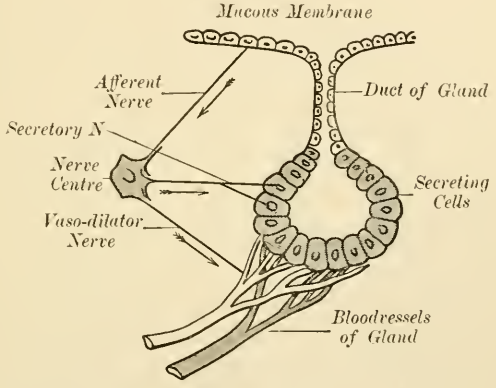


Diagram of a salivary gland and nerves. (LANDOIS.)

If the submaxillary and sublingual glands be cleanly dissected out, as in a living dog, for example, in which the glands are very accessible, they will be seen to be comparatively at rest, secreting little or no saliva, and their venous blood of a dark hue. If now a drop of vinegar be placed upon the tongue of the animal, at once the arterial twigs enlarge, the blood flows more rapidly, the veins pulsate, the color of their blood becomes scarlet, and the pressure increases, followed by an abundant discharge of limpid, very alkaline saliva, the so-called chorda tympani saliva, containing small quantities of albumin, globulin, mucin. That the phenomena just described are due to impressions transmitted to the medulla by the afferent sensory fibers of the lingual branch of the inferior maxillary and glosso-pharyngeal nerves, and thence reflected back to the submaxillary and sublingual glands by the efferent secreto-motor fibers of the chorda tympani (Fig. 354), is shown by such facts as that, after division of the lingual branch, the secretion of saliva, etc., ceases, but recommences if the central end of the divided nerve be stimulated. On the other hand, if the chorda tympani be divided,

the vessels supplying the submaxillary and sublingual glands contract; owing to the unopposed action of the sympathetic vaso-constricting fibers, the blood flows slowly, is diminished in quantity, and becomes dark, the secretion of saliva diminishes; the application of vinegar no longer excites the secretion. That the secretion does not altogether cease after division of the chorda tympani appears to be due to the independent reflex action of the submaxillary ganglion. If now, however, the divided chorda tympani be stimulated at its distal end, all the former phenomena recur. It may be mentioned, in this connection, though anticipated somewhat, that if the sympathetic plexus surrounding the facial artery be stimulated, the blood vessels of the glands become very much contracted, the blood flowing more slowly, and darker in color in the veins, and that the saliva then secreted—the so-called sympathetic saliva—is not only diminished in quantity, but contains, in addition to albumin and mucin, sarcode-like bodies. With division of the sympathetic fibers, the secretion of saliva does not altogether cease, a small quantity of the so-called paralytic saliva being secreted, if the tongue be stimulated with induced electricity.

The fact that an abundant supply of chorda saliva accompanies increased blood flow, a scanty supply of sympathetic saliva or diminished one would naturally suggest the idea that the secretion of saliva was simply a vasomotor effect, dependent upon the quantity and pressure of the blood. That such is not the case, however, that the phenomenon depends upon the stimulation of the salivary glands by secretory nerves is shown by the following considerations: That the pressure in the duct is greater than in the artery supplying the gland; that the temperature of the gland rises; that the amount of carbon dioxide is increased; that, after the injection of atropine into the gland, stimulation of the chorda tympani will still cause vascular dilatation, though no secretion. Just as there are involved in the production of saliva two sets of nerve fibers, secretory and vaso-dilator, so it is held by many physiologists that there are two kinds of secretory fibers, the secretory fibers proper, whose function it is to regulate the production of water and inorganic salts, and trophic fibers, which cause the formation of the organic constituents of the saliva. While it is possible that such a distinction exists as that of secretory and trophic fibers it cannot be said as yet to have been positively established.

In concluding our account of the functions of the facial nerve it remains for us now briefly to call attention to its external branches. Immediately after the nerve passes out of the stylo-mastoid foramen, as already mentioned, it sends a branch to the glosso-pharyngeal, upon which, as we shall see, the motor properties of the latter nerve depend. The posterior auricular branch receiving sensory filaments from the cervical plexus supplies the attolens and retrahens aurem and the posterior portion of the occipito-frontalis muscle

and the adjacent integument. The branches supplying the posterior belly of the digastric, stylo-hyoid, and stylo-glossus muscles are important, as these muscles are involved in mastication and deglutition. The temporo-facial branch, as we have seen, supplies all the muscles of the upper part of the face. If this branch be paralyzed, the eye remains therefore constantly open, through paralysis of the orbicularis palpebrarum muscle, and may become inflamed in consequence from constant exposure. The frontal portion of the occipito-frontalis, attrahens aurem, and the corrugator supercilii are also paralyzed. A striking symptom of paralysis of the facial nerve if these filaments be affected, is inability to corrugate the brow upon one side, as in frowning. Through paralysis of the muscles that dilate the nostrils olfaction and inspiration are also somewhat interfered with. To appreciate the influence exerted by the facial nerve upon inspiration it may be mentioned that in the horse, where the breathing is entirely nasal, death from suffocation very soon takes place if both facial nerves be divided, both nostrils then collapsing and becoming closed with each inspiratory effort.[1] The effect of paralysis of the facial nerve is well seen in cases of facial palsy affecting one side, the distortion of the features being due in such cases to the unopposed action of the muscles upon the unaffected side. When the paralysis is complete the angle of the mouth is drawn to the sound side, the eye on the affected side is widely opened, even during sleep, the lips are paralyzed upon one side, the saliva frequently flowing from the corner of the mouth while the food tends to accumulate between the teeth and cheek through paralysis of the buccinator, mastication in consequence being materially interfered with. If both facial nerves be paralyzed, mastication becomes very difficult, and the face exhibits a peculiarly expressionless appearance.

The Ninth Nerve.

The next nerve in order, the ninth or glosso-pharyngeal, the consideration of the eighth nerve or auditory being deferred for the present, arises in common with the nucleus of the pneumogastric from a column of cells (Fig. 337, *IX*) deeply situated beneath the lower and outer part of the floor of the fourth ventricle.

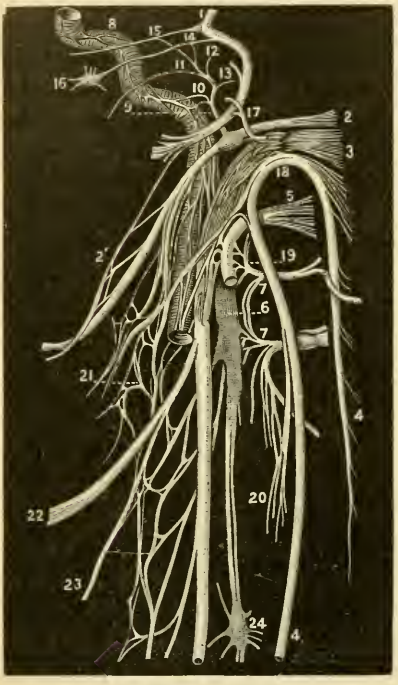
The nucleus appears to be in relation with axis-cylinders that are supposed to descend from motor cells of the opposite hemisphere, the locality of which is as yet ill-defined, and passing probably near the pyramidal tract cross the middle line to terminate in the medulla. After emerging from the medulla, the fibers of the glosso-pharyngeal proceed forward and outward by a series of five or six roots, containing about 9000 fibers, attached to the surface of the restiform body, the highest being close to the auditory nerve and passes out

[1] Bernard, Leçons sur la physiologie et la pathologie du Systeme Nerveux, Tome ii., p. 308. Paris, 1858.

of the cranial cavity through the jugular foramen (Fig. 355), in company with the pneumogastric and spinal accessory nerves. As the glosso-pharyngeal nerve passes out of the jugular foramen, it expands into the petrous ganglion or ganglion of Andersch from which fine filaments are given off to the pneumogastric and sympathetic nerves. The ganglion gives origin also to the tympanic or Jacobson's nerve; the latter, ascending through the canal of the same name in the petrous portion of the temporal bone, expands upon the promontory of the tympanum into a number of branches which supply the lining membrane of the tympanum, the round and oval windows, and the Eustachian tube. The tympanic nerve gives off also two small branches which pass respectively to the large and small petrosal nerves and filaments to the sympathetic plexus of the internal carotid artery. From the ganglion of Andersch the glosso-pharyngeal nerve descends between the jugular vein and the internal carotid artery to the root of the tongue on the inner side of the stylo-pharyngeus muscle terminating in the muscles and mucous membrane of the pharynx, soft palate, tonsils, the root and mucous membrane of the tongue, including the circumvallate papillæ.

During its course the glosso-pharyngeal sends off filaments to the pneumogastric and sympathetic, and as already mentioned, receives filaments from the facial.

Fig. 355.



The last four cerebral nerves: the facial nerve, the sympathetic and the upper two cervical nerves. 1. Facial nerve. 2. Glosso-pharyngeal. 2'. Anastomosis between a branch of the facial and the glosso-pharyngeal. 3. Vagus. 4. Accessory. 5. Hypo-glossal. 6. First cervical ganglion of the sympathetic. 7. First and second cervical nerves. 8. Cavernous plexus of the sympathetic on the internal carotid artery. 9. Tympanic nerve from the petrous ganglion of the glosso-pharyngeal. 10. Its connection with the carotid plexus. 11. Branch to the Eustachian tube. 12, 13. Branches to the oval and round windows of the ear. 14, 15. Branches joining the small and superficial petrosal nerves. 16. Otic ganglion. 17. Auricular branch from the jugular ganglion and the facial nerve. 18. Anastomosis of the accessory with the vagus. 19. Anastomosis of the first cervical nerve with the hypo-glossal. 20. Anastomosis of the second cervical nerve with a branch of the accessory. 21. Pharyngeal plexus. 22. Superior laryngeal nerve. 23. Its external branch. 24. Second cervical ganglion of the sympathetic. (Hirschfeld-Sappey.)

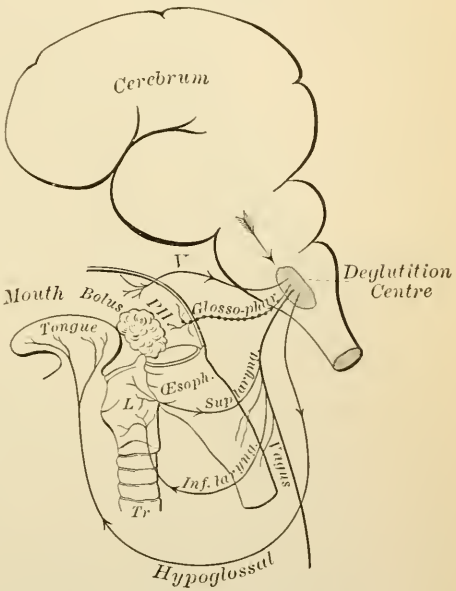
The glosso-pharyngeal nerve appears from recent researches to consist of three sets of fibers, sensory, gustatory, and motor,[1] origi-

[1] Obersteiner, op. cit., s. 294, s. 423.

nating in distinct parts of the nucleus of origin in the medulla, some of the motor fibers being derived, however, from the branch of the facial that joins the glosso-pharyngeal nerve at the petrous ganglion.

That the glosso-pharyngeal nerve is a sensory nerve, at least at its origin, is shown by the loss of sensibility in the parts to which it is distributed and loss of the sense of taste in the posterior third of the tongue following its division in a living animal or paralysis in man, and that stimulation at the root in a living animal fails to produce muscular contractions. Owing, however, to it containing motor fibers derived as already mentioned from its nucleus, as well as to its connections with the facial, the glosso-pharyngeal undoubtedly receives motor fibers, to which are due the muscular contractions following irritation of the glosso-pharyngeal when stimulated outside of the cranium, and the difficulty experienced in deglutition, if the nerve be divided in an animal, or be paralyzed in man. It has already been mentioned that the contractions of the muscles involved in deglutition following stimulation of the glosso-pharyngeal are reflex in character, the impressions made upon the latter nerve, like those made upon the palatine branches of the fifth nerve, being transmitted to the deglutition center in the medulla (Fig. 356) and thence reflected through the petrosal nerves to the ganglion of Meckel, and the otic ganglion to the muscles supplied by the latter.

Fig. 356.



Schema of the afferent and efferent nerves concerned in deglutition. (STIRLING.)

It will be seen from the above description that the glosso-pharyngeal nerve is a sensory nerve, endowing the tongue and pharynx with sensibility, and the posterior third of the tongue, and the anterior two-thirds as well, with the sense of taste, if the chorda tympani be regarded, as already mentioned, as a continuation of the pars intermedia, and the latter a branch of the glosso-pharyngeal. If it be admitted that the glosso-pharyngeal nerve contains specific motor fibers it must be regarded then as a motor as well as a sen-

sory nerve, independently of its connections with the facial. In conclusion it may be mentioned that the glosso-pharyngeal nerve possesses also inhibitory functions, diminishing or arresting the action of the cardio-motor, respiratory, and vasomotor centers of the medulla.

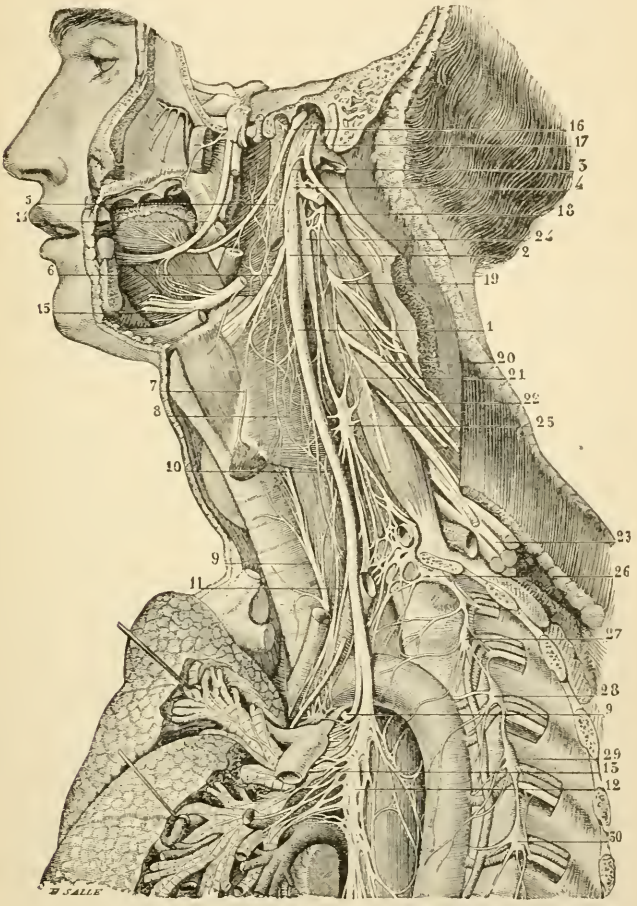
The Tenth Nerve.

The tenth nerve, the pneumogastric, par vagum, or vagus, arises as already mentioned, in common with the glosso-pharyngeal from a group of nerve cells situated beneath the lowest part of the floor of the fourth ventricle, giving rise to a promontory on the surface of the latter (Fig. 337, *X*). At the point of the calamus scriptorius, the symmetrically disposed nuclei are in contact at the middle line, but a little higher up are separated by the nuclei, giving origin to the hypo-glossal nerves. From this origin the fibers pass forward through the medulla, emerging by twelve or more roots containing about 9000 fibers attached to the restiform body in a line below those of the glosso-pharyngeal nerve, and leave the cranial cavity, as already mentioned, in company with the glosso-pharyngeal, spinal accessory nerves, and the internal jugular vein. In the jugular foramen the pneumogastric nerve presents a well-marked enlargement from one-sixth to one-fourth of an inch in length, the ganglion of the root or the jugular ganglion, from which pass filaments to the facial, and the ganglion of the glosso-pharyngeal and superior cervical ganglion of the sympathetic. After leaving the cranial cavity the pneumogastric nerve presents another enlargement from half an inch to an inch in length, the ganglion of the trunk, from which filaments pass to the hypo-glossal nerve and occasionally to the arcade formed by the first two cervical nerves. Immediately after leaving the cranial cavity the pneumogastric nerve receives an important branch from the spinal accessory, and during its course filaments from the first two cervical nerves, and together with fibers from the glosso-pharyngeal, spinal accessory, and sympathetic forms the pharyngeal plexus. That the pneumogastric is exclusively sensory at its origin, whatever may be the functions of its branches, appears to be satisfactorily shown, even though indirectly, by experiments like those of Longet[1] made upon horses and dogs just dead, in which stimulation of the nerve at its root failed to produce muscular contractions if the nerve was carefully insulated and all its motor connections divided. That irritation should be followed by muscular contractions if the latter precaution be not observed, should not excite surprise when it is remembered that the pneumogastric receives motor filaments from at least five sources, viz., the facial, spinal accessory, hypoglossal, and first and second cervical nerves, not to speak of the motor fibers derived from the sympathetic. Any muscular contractions ensuing upon irritation of the pneumogastric

[1] Physiologie, Tome iii., p. 508. Paris, 1869.

must therefore be either reflex in character like many of those of the glosso-pharyngeal already referred to, or be attributed to the stimulation of fibers derived from the motor sources just mentioned.

FIG. 357.



Distribution of the pneumogastric. 1. Trunk of the left pneumogastric. 2. Ganglion of the trunk. 3. Anastomosis with the spinal accessory. 4. Anastomosis with the sublingual. 5. Pharyngeal branch (the auricular branch is not shown in the figure). 6. Superior laryngeal branch. 7. External laryngeal nerve. 8. Laryngeal plexus. 9, 9. Inferior laryngeal branch. 10. Cervical cardiac branch. 11. Thoracic cardiac branch. 12, 13. Pulmonary branches. 14. Lingual branch of the fifth. 15. Lower portion of the sublingual. 16. Glosso-pharyngeal. 17. Spinal accessory. 18, 19, 20. Spinal nerves. 21. Phrenic nerve. 22, 23. Spinal nerves. 24, 25, 26, 27, 28, 29, 30. Sympathetic ganglia. (HIRSCHFELD.)

The most important branches given off by the pneumogastric (Fig. 357), whose functions we shall study seriatim, are as follows: the meningeal, auricular, pharyngeal, superior and inferior laryngeal, cervical and thoracic, cardiac, anterior and posterior pulmonary, œsophageal, and abdominal.

The first or meningeal branch of the pneumogastric nerve is given off from the jugular ganglion and passes with the vasomotor fibers of the sympathetic supplying the middle meningeal artery to the occipital and transverse sinuses. It is usually regarded as consisting of sensory fibers.

The auricular, or Arnold's nerve, though containing fibers derived from the facial and glosso-pharyngeal nerves, is usually described as being a branch of the pneumogastric nerve, being given off from the ganglion of its trunk. Passing through the temporal bone by the canal of the same name, it is distributed to the external auditory meatus and the membrana tympani, endowing those parts with sensibility. The pharyngeal branches are given off from the superior portion of the ganglion of the trunk of the pneumogastric nerve, but consist largely of filaments derived from the spinal accessory, reinforced, further, during their course, by filaments from the glosso-pharyngeal and superior cervical ganglion of the sympathetic to form the pharyngeal plexus, which supplies the muscles and mucous membrane of the pharynx, the motor filaments being derived, as we shall see, from the spinal accessory, and the sensibility being due to the filaments of the pneumogastric proper, and also to those of the pharyngeal branches of the fifth, and of the glosso-pharyngeal.

The superior laryngeal nerve arising from the ganglion of the trunk divides into the external and internal branches, the external branch receiving filaments from the inferior laryngeal, and the sympathetic supplies the mucous membrane of the ventricle and crico-thyroid muscles of the larynx, and the inferior constrictor of the pharynx. The internal branch, also receiving filaments from the inferior laryngeal, supplies, like the external branch, the crico-thyroid muscles, and is distributed to the mucous membrane of the epiglottis, the base of the tongue, the aryteno-epiglottidean folds, and the mucous membrane of the larynx as far down as the true vocal membranes. From the anatomical disposition it might be inferred that the general sensibility of the upper part of the larynx and the surrounding mucous membrane, as well as the innervation of the crico-thyroid muscle, was due to the superior laryngeal nerve, and experiment shows that such is the case. Thus, stimulation of the superior laryngeal nerves in a living animal gives rise to intense pain, and causes contraction of the crico-thyroid muscle. It is through the exquisite sensibility of the upper part of the mucous membrane of the larynx that foreign bodies are prevented from entering the air passages; impressions made by such, being transmitted to the medulla, are thence reflected through the inferior laryngeals back to the larynx, bringing about a closure of the glottis. Every one is familiar with the fact that if a crumb of bread, etc., fall upon the aryteno-epiglottidean folds or the edge of the vocal membranes, the sensibility of the parts is such as to excite a convulsive cough, by which the foreign body is dislodged and expelled. The impression conveyed by the superior laryngeal

nerve to the cough center of the medulla being reflected thence through the nerves supplying the expiratory muscles of the chest and abdomen, by which the coughing is accomplished. That this reflex action is due to the sensibility of the laryngeal mucous membrane is shown by the fact that, after division of the superior laryngeal nerve, impressions made upon the mucous membrane fail to bring about such action. The superior laryngeals, also, constitute the afferent nerves in the reflex mechanism by which, through contraction of the constrictors of the pharynx, the act of deglutition is completed. It is interesting to observe that the impressions made upon the mucous membrane of the larynx, and the surrounding membrane, and by which, through reflex action, deglutition is brought about, cause, at the same time, closure of the glottis, and arrest of respiration, thereby protecting the air-passages against the entrance of food or other foreign bodies.

The two inferior or recurrent laryngeal nerves, so called from reascending to the larynx after descending from the pneumogastric, differ slightly in their course on the two sides, that of the left side passing beneath the aorta, that of the right side winding from before backward around the subclavian artery before they ascend in the groove between the trachea and the œsophagus to the larynx. In other respects, the course and distribution of the two nerves are the same. The curious course taken by the inferior laryngeal nerve, whether of the right or left side, is due to the fact that, while in the embryonic condition, the larynx and heart are in close proximity; through the elongation of the neck, incidental to development, the heart and great blood vessels recede from the larynx, and, in so doing, drag down with them the inferior laryngeal nerves, which pass, loop-like, around them. It may be mentioned in this connection, as observed by Owen,[1] and by the author,[2] in the individuals dissected by the latter, that in the giraffe the inferior laryngeal nerves pass directly from the pneumogastric to the larynx, like the superior laryngeals. The significance of this is very evident, for, were the course of the inferior laryngeals in the giraffe the same as in man, the nerve, in descending and ascending through so many feet, would, in all probability, be so stretched and tensed as to render it incapable of performing its functions. As the inferior laryngeal nerves ascend they give off filaments, which join those of the cardiac branches of the pneumogastric filaments to the muscular tissue, and mucous membrane of the upper part of the œsophagus, to the mucous membrane and inter-cartilaginous muscular tissue of the trachea, to the inferior constrictor of the pharynx, and, as already mentioned, a branch which joins the superior laryngeal, terminating, finally, after penetrating the larynx behind the posterior articulation of the cricoid, with the thyroid cartilage, in all of the intrinsic muscles of the larynx, except the

[1] Op. cit. Vol. iii., p. 160.
[2] H. C. Chapman, Proc. Acad. Nat. Sciences, Phil., 1887, p. 37.

crico-thyroid, which, it will be remembered, is supplied by the superior laryngeal nerve. Direct stimulation of the inferior laryngeal nerves proves what one would be led to expect from their distribution, that they are principally motor in function, and from the fact, as we shall see hereafter, of division of the spinal accessory being followed by loss of voice, the respiratory movements of the glottis being, however, unaffected, but that division of the inferior laryngeal nerves not only involves loss of voice, but paralysis of the respiratory movements of the larynx as well—that their motor filaments are derived at least from two different sources, if not more. To anticipate what we shall see more particularly hereafter, the muscles of the larynx involved in the production of the voice are the arytenoid, the thyro-arytenoid, and the lateral crico-arytenoid, supplied by the inferior laryngeal nerves and the crico-thyroid, supplied by the superior laryngeal nerves. The posterior crico-arytenoid muscles supplied by the inferior laryngeal nerves opening the glottis, are, however, respiratory in function. Now, while in an animal the voice is lost after division of the internal branch of the spinal accessory, nevertheless, the glottis, though not closing on irritation, being still capable of dilatation, respiration is not interfered with. Such being the case, if the inferior laryngeal, however, be divided, the glottis is at once mechanically closed with each inspiratory effort, and the animal, if young, dies of suffocation. In adults, however, the cartilages of the larynx, being rigid, permit of respiration even after the larynx is paralyzed. The only inference from these facts is that the fibers of the inferior laryngeal that innervate the muscles of phonation are derived from the spinal accessory, but that those innervating the respiratory movements of the glottis are derived from some other source—from the facial, in all probability, or, possibly, from the hypo-glossal, or the cervical nerves that we have seen give off branches to the pneumogastric nerve. Inasmuch, also, as the crico-thyroid muscle is involved in phonation, and as we have seen that the superior laryngeal nerve supplying it receives fibers from the inferior laryngeal, in all probability it is the fibers of the latter nerve that influence the crico-thyroid muscle in phonation, otherwise it is difficult to see why the paralysis of the voice following division of the inferior laryngeal nerve should be so complete.

It must be admitted, however, that the view just offered of the functions of the laryngeal nerves is not universally accepted. Indeed, considerable difference of opinion still prevails among physiologists as to exactly how the different parts of the larynx are innervated.

The cervical cardiac branches, two or three in number, arising from the pneumogastric, consist principally, as we shall see, of fibers derived from the sympathetic. **The thoracic cardiac** branches given off below the origin of the inferior laryngeal nerves pass to the cardiac plexus.

The Innervation of the Heart. Intracardiac Centers and Nerves.

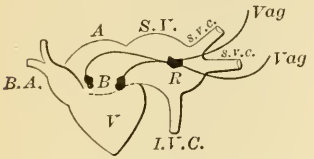
It is well known that the heart of the lower vertebrates, like the shark, sturgeon, etc., will continue beating for many hours after removal from the body. The same has been shown to be true also of the heart of rabbits, cats, dogs when proper precautions are taken.[1] Such facts show conclusively that the cause of the rhythmical beat of the heart, being independent of the central nervous system, must lie within the heart itself. Difference of opinion still prevails, however, as to whether the beat of the heart is due to the heart muscle possessing the power of rhythmical contraction in itself, or to the heart muscle being periodically stimulated by impulses from the intracardiac cells. That the latter is the cause of the rhythmical beat of the heart appears to be shown from the fact that the contractions are more powerful in those parts of the heart in which the nerve supply is richest. Thus the contractions of the auricle are more powerful than those of the ventricle, those of the base of the ventricle more so than those of the apex, the number of nerve cells being greatest in the auricle, smallest in the ventricle. Indeed, in the apex of the ventricle ganglion cells are entirely absent according to most histologists. It may be also mentioned as confirmatory of the view that the cause of the heart beat is nervous in origin, that while muscarin arrests the contractions of the muscular fibers of the heart it does not exert the same influence upon other kinds of either striped or smooth muscle. On the other hand, there can be no doubt that the muscular fibers of the heart respond to stimuli other than nervous, since a slip cut from the ventricle of the heart of a tortoise, when suspended in a moist chamber, will begin beating in a few minutes and continue to beat for more than twenty-four hours. The nerve fibers that are supposed to convey the impulses stimulating the muscular fibers to contract, appear to arise in ganglia situated near the orifice of the superior vena cava, in the septum of the auricles and in the auriculo-ventricular grooves, whence they pass as fine non-medullated fibers to penetrate the walls of the auricles and ventricles. The ganglia of the heart, at least in the case of the frog, appear to have antagonistic functions, some of the ganglia, for example, inhibiting the functions of the other. The presence of cardiac ganglia can be readily demonstrated in the heart of the frog, and their functional significance shown by the well-known experiment of Stannius.[2] In the frog, as is well known, the two superior venæ cavæ (*SVC*, Fig. 358) unite before entering the right auricle to form a dilatation—the sinus venosus (*SV*). It is in the wall of the latter, near the opening of the inferior vena cava, that the first of these ganglia, the ganglion of Remak (*R*), is situated, the second or the ganglion of Bidder (*B*), being found in the

[1] Stolnikow, Pawlow, Langendorff in Tigerstedt, Lehrbuch Der Physiologie Des Kreislaufes, 1893. [2] Zwei Reihen, Physiologische, Versuche, 1851.

left auriculo-ventricular groove, the third ganglion or that of Ludwig, in the septum between the auricles.

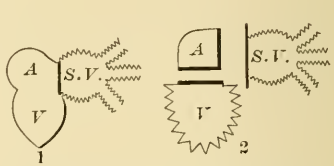
If a ligature be applied between the sinus venosus (*S V*) and the right auricle (*A*, Fig. 359, 1), the heart stops beating and remains in a state of diastole.

Fig. 358.



Schema of nerves of frog's heart. *R*, Remak's, and *B*, Bidder's ganglia. *SV*. Sinus venosus. *A*. Auricles. *V*. Ventricle. *B.A*. Bulbus arteriosus. *Vag*. Vagi. *SVC*, superior venæ cavæ. (Landois.)

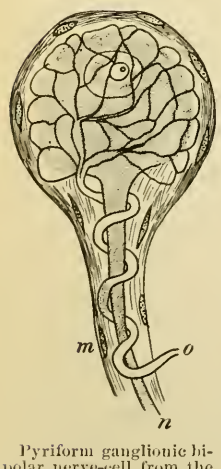
Fig. 359.



Stannius' experiment. *A*. Auricle. *V*. Ventricle. *SV*. Sinus venosus. The zig-zag lines indicate which parts continue to beat; in 2 the ventricle beats at a different rate. (Landois.)

The sinus venosus, however, continues beating, and the auricles or the ventricle will made a few movements in response to direct stimulation. If now a second ligature be applied between the auricle (*A*), and ventricle (*V*, Fig. 359, 2), the ventricle will begin beating again, the auricles, however, still remaining quiet. Many explanations have been offered of the phenomenon just described, one of the simplest and most plausible being that which regards the ganglion of Ludwig as inhibitory in function and exerting greater influence than that of Remak or Bidder, when either of these ganglia is exerted alone. If such be the case, it follows that a ligature being applied to the sinus venosus (Fig. 359, 1), the inhibitory action of the ganglion of Ludwig being only opposed to the exciting action of that of Bidder, the heart stops, and that after a ligature is applied between the auricles and the ventricle (Fig. 359, 2), then the inhibitory action of the ganglion of Ludwig being cut off, and there being nothing to counteract the action of the ganglion of Bidder, the ventricle begins to beat again. Whatever the explanation may be of the facts just described, it is evident that the heart possesses an intrinsic nervous mechanism by which, in response to the stimulus, its fibers are excited to contract.

Fig. 360.



Pyriform ganglionic bipolar nerve-cell from the heart of a frog. *m*. Sheath. *n*. Straight process. *o*. spiral process.

It may be mentioned in this connection that many of the ganglionic nerve cells of the heart of the frog present not only an axis-cylinder, but a spiral process as well (Fig. 360, *o*), of functional interest since the process appears to be derived from the pneumogastric nerve and to convey impulses to the nerve cell.

If non-polarizable electrodes be applied to the surface of the ventricle of a frog's heart and connected with a delicate galvanometer, it will be observed that with each ventricular systole the needle of the galvanometer is deflected, returning to rest with each diastole, showing that a change in electrical potential precedes or more probably accompanies the change in form that has been described as a cardiac contraction. Further, if one electrode be applied to the base of the heart and the other to the apex it will be found that this change in electrical potential, "the current of action," the excitation wave travels from base to apex at the rate of from 50 to 150 millimeters per second and preceded according to some observers by a latent period of about 0.08 sec.[1] Some difference of opinion still exists as to whether the excitation wave passes along the muscular or nervous tissues of the heart. From the fact that the wave travels comparatively slowly, about 90 millimeters per second or 300 times[2] less than at the rate at which it would travel if it were transmitted by nervous tissue, it is generally supposed that the wave travels along the muscular rather than along the nervous tissue. That the excitation wave travels along the muscular fiber is still further shown by the fact that the "block,"[3] or the delay that the wave experiences in passing from the auricle to the ventricle, appears to depend upon the relatively few fibers present in that situation, and that the duration of the "block" is about what it ought to be on the supposition that the wave passes along the muscular fibers connecting the auricles and ventricle.

It is well known that, while the heart will contract in response to mechanical and electrical stimuli when slowly repeated, it will not contract when the stimuli follow each other too rapidly. This appears to be due to the fact that the heart will not contract secondarily in response to an extra stimulus when applied during the period intervening between the beginning and maximum of its systole, whereas it will contract secondarily when the stimulus is applied during the period intervening between the maximum of one systole and the beginning of the next.[4] The period of the cardiac cycle during which the heart refuses to contract in response to a stimulus is called the "refractory period." Since a period exists however in which the heart will contract in response to a stimulus it might be supposed that if the stimulus be rapidly applied during that period, that is during the "non-refractory period," on account of the extra contraction produced with each stimulus, the total number of contractions would be increased. As a matter of fact, however, such is not the case, as the extra con-

[1] Engelmann, 1874, p. 6.

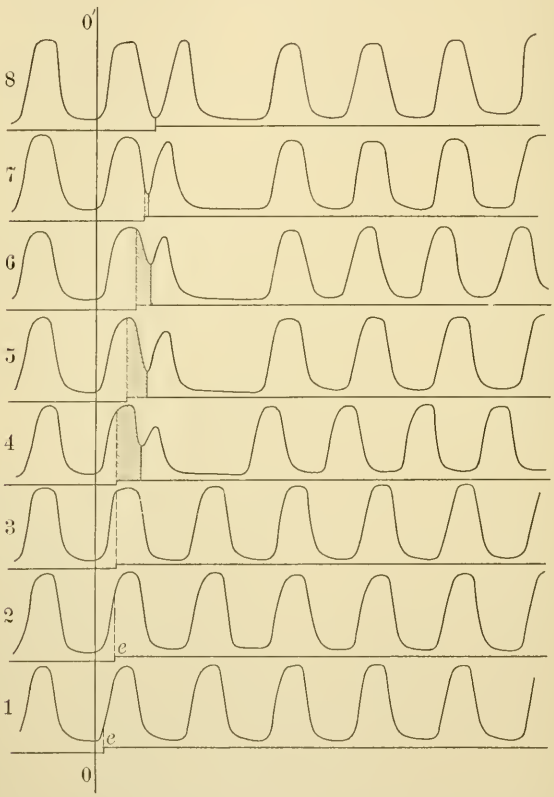
[2] The author takes occasion to say that by throwing a beam of light upon the mirror of the galvanometer and reflecting the same upon a screen he has been able to demonstrate the "current of action" of the frog's heart to a large audience, the ball of light moving pendulum-like with the systole and diastole of the heart.

[3] Gaskell, Journal of Physiology, Vol. iv., p. 95.

[4] Marey, 1876, p. 73. Engelmann, 1895, p. 313.

traction is followed by a pause, the duration of which, being that of the normal pause plus the interval between the appearance of the extra contraction and what would have been the end of the cardiac cycle in which the extra contraction occurred, the normal number of contractions is maintained. The pause following the extra contraction induced during the "non-refractory period" is appropriately called therefore the "compensatory pause." It follows from

FIG. 361.



The refractory period and compensatory pause. Curves to be read from left to right. The interruption on the abscissa below each curve indicates the moment at which the ventricle was stimulated. In the curves 1, 2, 3, the ventricle was refractory to the stimulus, the latter being applied during the refractory period. In the remaining curves an extra contraction and compensatory pause are seen, the stimulus having been applied after the refractory period. (MAREY.)

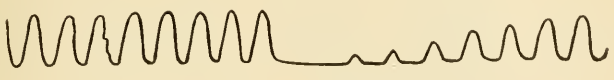
what has just been said that a continuous stimulus may produce a rhythmical heart beat, since, the heart contracting only during the "non-refractory period," each contraction will be followed by a compensatory pause. That the refractory period and compensatory pause are produced independently of the cardiac nerve centers appears to be shown from the fact that both can be obtained when the

apex of the ventricle is used in which it is generally supposed, as already mentioned, that nerve centers are absent.

Extracardiac Inhibitory Centers and Nerves.

Contrary to what might have been naturally expected from what we have hitherto learned as to the effect of division and stimulation of nerves, division of the pneumogastric nerve in a living animal, so far from arresting the action of the heart, actually increases the rapidity of its pulsations, while electrical stimulation of the pneumogastric nerve arrests the heart's action in diastole (Fig. 362), and causes a fall in the blood pressure (Fig. 363).

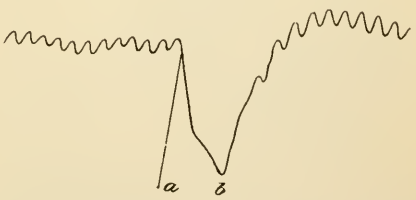
Fig. 362.



Effect of stimulation of pneumogastric nerve upon action of heart in frog. To be read from right to left.

The effect of division of one pneumogastric nerve, however, in a frog or a rabbit, for example, is not by any means as marked as when both nerves have been divided. In the latter case the action of the heart is tremulous, the number of its beats may be doubled, while the respiration, from being momentarily accelerated, becomes calm and profound, but diminished in frequency. It might naturally be supposed that the inhibitory influence of the cardiac fibers of the pneumogastric is directly exerted upon the heart. That such, however, is not the case, appears from the fact of the latent period—that is, the time elapsing between the application of the stimulus and the inhibitory effect—being very long, nearly one-fifth of a second, instead of one-hundredth of a second, in some cases even two entire beats of the heart intervening before its arrest occurred, indicating that some resistance must be overcome, the inhibitory fibers of the pneumogastric acting upon inhibitory centers in the heart itself. That such is the case is shown by the fact that the action of the heart in the eel and the frog can be arrested by direct stimulation, and that in the mollusca, although no pneumogastric nerve is present, the heart can be stopped in diastole by direct irritation. Again, if nicotin or curara be subcutaneously injected

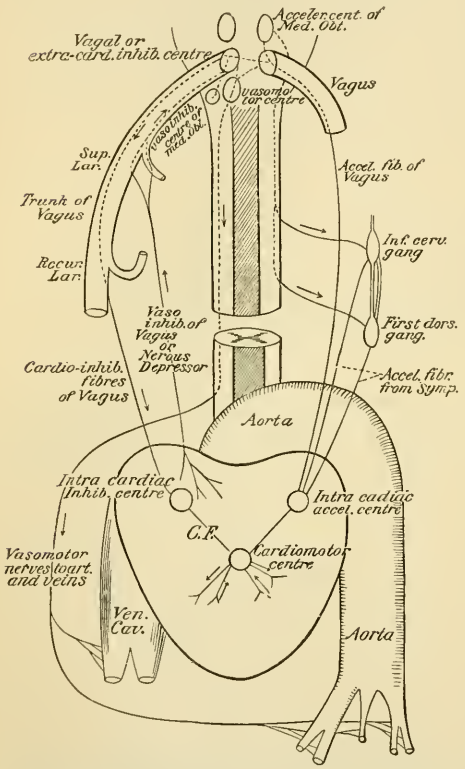
Fig. 363.



Effect of cardiac inhibition in rabbit on blood pressure. Current sent into pneumogastric nerve at *a*, shut off at *b*. First, there is a rapid fall, and when the heart beats return, the mercury rises by successive leaps to the normal.

in small doses into a living animal the heart beats first slower then faster, possibly on account of the extracardiac inhibitory centers of the pneumogastric (Fig. 364) becoming paralyzed; if now muscarin or jaborandi be then administered, the heart will be arrested in diastole, the latter substances appearing to act directly upon intracardiac inhibitory centers. On the other hand, if atropia be injected, then neither muscarin nor jaborandi will have any inhibitory effect upon the heart, atropia appearing to paralyze both the extra- and intracardiac inhibitory centers.

FIG. 364.



Diagrammatic view of the nerves influencing the action of the heart. The right half represents the course of the inhibitory, and the left the course of the accelerating nerves of the heart; the arrows showing the direction in which impressions are conveyed. The ellipse at the upper extremity of the vagus looking like the section of the nerve is intended to represent the vagal nucleus or center. In this diagram the nerves are incorrectly made to cross, instead of passing behind, the aorta.

Stimulation of the pneumogastric nerve not only inhibits the heart's action but modifies the latter in many ways. Thus the duration of both the systole and diastole are lengthened. The force of the contraction, the input and output of the ventricle are diminished, the diastolic pressure and volume of the blood in the ventricle are increased. The contractions of the ventricle do not correspond in number to those of the auricle, the latter being often twice as numerous as the former. A change in electrical potential occurs also, the current of rest of the injured auricle of a tortoise heart lead off to a galvanometer exhibiting a marked increase. It may be mentioned in this connection that the act of swallowing temporarily abolishes the inhibitory action of the vagus, the pulse rate being accelerated often 30 per cent. by merely sipping a wineglassful of water. That the influence exerted by the fibers of the pneumogastric nerve upon the heart is transmitted centrifugally and is dependent upon its motor fibers is shown by the fact that if the pneumogastric nerve be divided in a living animal and stimulated

at its central end none of the effects such as those just described ensue; stimulation of the distal end only slowing up the action of the heart and causing a fall in blood pressure; and that if the stimulation be continued too long, so as to exhaust the irritability of the motor fibers, the heart begins to beat again, their inhibitory effect being lost.[1] Further, in animals poisoned with curara, which, as is well known, paralyzes the motor nerves, stimulation of the pneumogastric nerve fails to arrest the action of the heart. That the motor fibers of the pneumogastric nerve influencing the heart's action are derived from the spinal accessory can be shown by experiments like those of Waller,[2] in which after division of the spinal accessory of one side in a living animal, allowing sufficient time to insure disorganization of its fibers, stimulation of the pneumogastric nerve of the corresponding side failed to arrest the action of the heart, the usual effect, however, being observed when the pneumogastric nerve was stimulated on the one side in which the spinal accessory nerve was still intact. It must be mentioned, however, that according to some experimenters, stimulation of the spinal accessory before its union with the pneumogastric nerve, or of its bulbar roots does not inhibit the heart's action and that the method employed by Waller just mentioned involves the pulling out of some of the fibers of the pneumogastric nerve. If such be the case it must be admitted that the origin of the inhibitory fibers of the vagus are still unknown. The fibers passing along the pneumogastric nerve and conveying inhibitory impulses to the heart are usually regarded as arising from a cardio-inhibitory center (Fig. 364), situated in the medulla oblongata near the nucleus of the hypo-glossal nerve. The cardio-inhibitory center appears to be a tonic center, that is, always acting, division of the pneumogastric nerve being followed as we have seen by quickening of the heart's action. The center seems to be maintained in this state of constant activity reflexly through impressions conveyed to it by afferent nerves, since the heart beat is not quickened by division of the pneumogastric if many afferent impulses are cut off, as is the case after division of the spinal cord. It is impossible in the present state of our knowledge to offer an entirely satisfactory explanation of the inhibitory effect of the pneumogastric nerve upon the heart and of the accompanying fall in blood pressure. A plausible explanation that has been offered is as follows:

A stimulus being applied to the central end of the vaso-inhibitory or depressor fibers of the vagus (Fig. 364), the impulse generated, as already mentioned, is not only transmitted to the extracardiac inhibitory centers, whence it is reflected through the cardio-inhibitory fibers of the pneumogastric nerve to the heart, slowing or arresting the latter, but also which exerts a restraining or inhibitory influence upon the vasomotor center of the medulla, the result of

[1] Weber, Archiv d'Anat. Gén. et de Physiologie, 1846.
[2] Gazette Médicale, 3ieme serie, Tome xi., p. 420. Paris, 1856.

which is that the blood pressure sinks through the inhibition of the vasomotor nerve fibers supplying the blood vessels, and which emanate from this center. To anticipate a little what will be described more in detail in our consideration of the sympathetic, it may be mentioned, with reference to the explanation just offered of the fall in blood pressure, that, under ordinary circumstances, a nervous influence emanates from the vasomotor center in the medulla, and which, being transmitted through the spinal cord, spinal and splanchnic nerves, maintains the blood vessels to which these nerves are distributed in a state of tonic contraction, which keeps up the blood pressure. If, however, the vasomotor center of the medulla be paralyzed through the stimulation of the depressor nerve, no such nervous influence being then exerted upon the blood vessels, the latter dilate, and the blood pressure falls. The result of this is, however, that the medulla receives less blood, so much passing into the abdominal vessels, etc., the consequence of which is, that the extracardiac inhibitory centers of the pneumogastric become less active, and the heart resumes its usual activity. That it is to the paralysis of the splanchnic nerve, and consequent dilatation of the great abdominal vessels, that the fall in blood pressure induced by stimulation of the depressor nerve is principally due, is shown by the fact that if the splanchnic nerves be first divided, and then the depressor nerve be stimulated, the blood pressure sinks but little more than when the splanchnics are alone divided.

That the cardiac branches of the pneumogastric nerves have the same inhibitory influence upon the heart in man as they have been shown experimentally to have in animals, may be inferred from such pathological[1] cases as those in which the number of heart beats have been known to be reduced to three or four per minute from the compression exerted upon the nerve by pressing upon glands, tumors, etc. That the inhibitory action of the pneumogastric upon the heart can also be exerted in a reflex as well as direct manner, is shown by those cases in which there is a sudden stoppage of the heart following blows upon the epigastrium, especially after full meals, draughts of cold water, the body being overheated, great emotional excitement, etc., the impression in such cases being transmitted from the general sensory surface to the medulla and thence reflected through the inhibitory fibers of the pneumogastric to the heart. That the pneumogastric nerve in man contains also special afferent fibers passing from the heart as well as efferent ones to it, by which impressions are transmitted to the medulla and thence reflected back to the heart by the inhibitory fibers, appears very probable from what has been shown to be experimentally the case in the rabbit and other animals. Thus, if in the rabbit, the so-called depressor nerve (Fig. 364)—that is, the nerve arising partly from the pneumogastric and partly from the superior laryngeal nerve, be divided and its distal end stimulated,

[1] Muller's Archiv, 1841, Heft 3. Jenæsche Zeits., 165, s. 384.

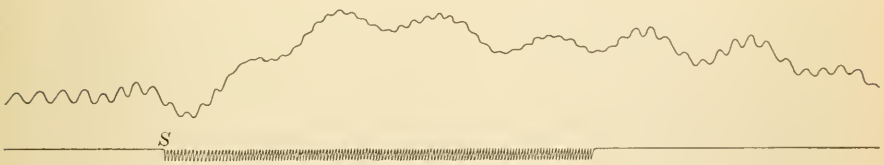
no effect upon the heart is observed; if, however, the central end of the nerve be stimulated, the action of the heart is arrested and the blood pressure falls just as if the pneumogastric nerve or the cardio-inhibitory fibers of the same (corresponding in man to the superior cardiac nerve) be stimulated, the action being evidently a reflex one; the impression made upon the central end of the depressor nerve is transmitted to the medulla and thence reflected back through the cardiac inhibitory fibers of the pneumogastric to the heart.

Extracardiac Accelerator Centers and Nerves.

The cardiac fibers of the pneumogastric nerve not only consist of inhibitory or restraining fibers, but also augmentor or accelerating ones (Fig. 364). The latter are, however, derived, to a considerable extent, also, from fibers, which, descending from the medulla through the spinal cord, emerge opposite the last cervical and first dorsal ganglia of the sympathetic, which they pass before terminating in the heart.

Stimulation of the augmentor nerves not only accelerates the heart's action (Fig. 365), but increases the force of the beat, the

FIG. 365.



Effect produced by stimulation of peripheral end of the accelerating nerve of the heart. The heart beats quicker. Stimulation begun at *S*. (LANDOIS.)

output, and the speed of the excitation wave. The accelerating nerves appear to act less powerfully than the inhibitory ones, at least the effect of simultaneous stimulation is inhibition, the amount of the latter being less, however, than when the inhibitory nerves are stimulated alone. Analogy would lead us to suppose that there exists an extracardiac accelerating center, situated probably in the medulla (Fig. 364), which acts upon the heart in a similar manner to that of the extracardiac inhibitory one. That such a center exists and is tonic in nature, ever acting, appears to be shown by the fact that the pulse rate is lowered by division of the vagi and subsequent bilateral extirpation of the inferior cervical and first thoracic ganglia. It is well known that stimulation of the intracardiac nerves by the application of acids to the surface of the heart gives rise to reflex actions, such as movements of the limbs, etc. That the impulses are conveyed by the vagi appears to be shown from the fact that such reflexes do not occur if the vagi are divided. The vagi are also supposed by some physi-

ologists to convey sensory impulses to the brain. If such be the case the sensations cannot be very acute since in cases like those of the Viscount Montgomery described by Harvey,[1] where the opportunity was afforded of feeling directly the heart the individual was entirely unconscious when his heart was touched.

Innervation of the Lungs.

The pulmonary branches of the pneumogastric nerve are given off as the anterior and posterior branches. The anterior pulmonary branches, after sending a few filaments to the trachea, form a plexus which, surrounding the bronchial tubes, is continued to the termination of the latter in the pulmonary air cells. The posterior pulmonary branches, larger and more numerous than the anterior ones, together with fibers derived from the upper three or four thoracic ganglia of the sympathetic, constitute the posterior pulmonary plexus. After giving off fibers to the inferior and posterior portion of the trachea, to the muscular tissue and mucous membrane of the middle portion of the œsophagus, to the posterior and superior portion of the pericardium, the posterior pulmonary plexus surrounds the bronchial tubes, and, like the anterior one, is continued with the latter to the air cells. The pulmonary branches of the pneumogastric nerve supply the lower part of the trachea, the bronchi, and the lungs, with both sensory and motor fibers, as shown by experiments like those of Longet,[2] in which, after division of the pneumogastric nerve in the neck, the mucous membrane of the trachea and bronchus became insensible, while stimulation of its branches caused the muscular fibers of the bronchus to contract.

Respiratory Center and Nerves.

The phenomenon of respiration, the principal features of which have been already described, is essentially an involuntary reflex one, involving the nice coördination of very complex muscular action, and depending upon the presence of a respiratory center in relation with afferent and efferent nerves. From the fact that respiration may continue after removal of all parts of the brain above the level of the bulb, but immediately ceases after the destruction of an area about 5 millimeters wide lying between the nuclei of the pneumogastric and hypo-glossal nerves, in the lower part of the calamus scriptorius it is supposed that the respiratory center, the "nœud-vital" of Flourens, is situated in the medulla. The respiratory center appears to consist of two halves symmetrically situated on either side of the middle line, but so intimately connected by commissural fibers that the two halves constitute physiologically but one center. That this is the case is shown by such facts as that the change in the character of the respiration follow-

[1] Exercitationes De Generatione Animalium, Londini, 1651, Exer. lii.
[2] Traité de Physiologie, Tome iii., p. 535.

ing division of one pneumogastric nerve, or stimulation of its central end is manifested upon the opposite as well as upon the injured side of the body. On the other hand, if the commissural fibers connecting the two halves of the respiratory center be divided, the two halves act separately independently of each other, yet synchronously. Each half of the respiratory center is further supposed by many physiologists to consist physiologically of two centers, inspiratory and expiratory, influencing the inspiratory and expiratory muscles respectively. As the inspiratory center increases the rate of respiration and the expiratory center diminishes it, the inspiratory center is regarded as being accelerator the expiratory as inhibitory, in nature. Both centers, however, arrest the respiratory movements in the inspiratory and expiratory phases respectively, if the stimulus be sufficiently powerful. Of the two centers the accelerating center appears to be the more irritable, hence if both centers be stimulated simultaneously, the effect will be accelerating. While there is no doubt that the respiratory movements are due to impulses arising in the respiratory center and transmitted periodically by efferent nerves to the respiratory muscles, difference of opinion still prevails as to what constitutes exactly the stimulus exciting the respiratory center to action. From the fact that rhythmical respiratory movements still persist even with removal of all parts of the brain above the bulb and after division of the vagi and glosso-pharyngeal nerves, of the spinal cord in the lower cervical region, and posterior roots, it is obvious that the respiratory center is susceptible of being excited by other stimuli than impulses transmitted by afferent nerves. In such exceptional cases and probably in all cases, the stimulus exciting primarily the respiratory center appears to be the blood,[1] the respiratory rhythm being, however, much modified by the influence exerted by the will, the emotions, and various afferent impulses. That the respiratory movements are greatly influenced, if not entirely due to the stimulus exerted by the blood is shown by the fact that the number of respirations are increased or diminished, and the rhythm modified in proportion as the blood is freely supplied or cut off, and according to its temperature, and the relative amounts of oxygen or carbon dioxide and products of muscular activity that it contains. That we can voluntarily modify to some extent, at least, our respiratory movements and that the latter are greatly affected by the emotions is familiar to all.

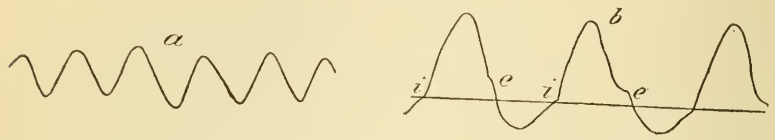
Afferent Respiratory Nerves.

The afferent respiratory nerves are the pneumogastric and its laryngeal branches, the glosso-pharyngeal, the trigeminus, and the cutaneous nerves generally. While division of the pneumogastric nerve on one side may not affect the respiration, as a general rule

[1] Loewy, Pflüger's Archiv, Band xliii., 1889, s. 245, 281.

the respiratory movements become slower, deeper, and longer; these effects being, however, only transient, the respiration soon becomes normal again. If the central end of the divided pneumogastric be stimulated, the effects following will depend upon the nature of the

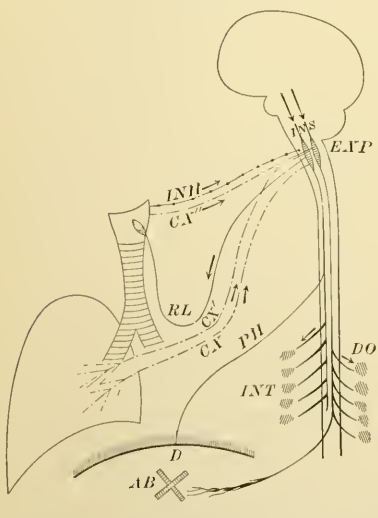
FIG. 366.



a. Tracing of the respiratory movements of the cat. *a*. Before. *b*. After division of both vagi.

stimulus. Thus, chemical stimuli excite expiration, mechanical stimuli inspiration, electrical stimuli expiration or inspiration, or both, according to the strength of the current. After section of both pneumogastric nerves, the respiratory movements become slower, deeper, more powerful (Fig. 366, *b*), the amount of air inspired being, however, the same, expiration active, with a pause following expiration. Expiration appears to be more readily produced by weak electrical stimuli than inspiration, a weak current when applied to the central end of the pneumogastric nerve, both nerves having been divided, exciting expiration, a strong current inspiration.

FIG. 367.



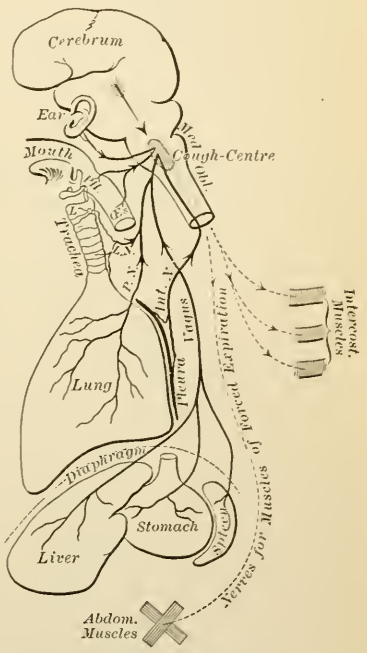
Schema of the chief respiratory nerves. *INS*, Inspiratory, and *EXP*, Expiratory center—motor nerves are in smooth lines. Expiratory motor nerves to abdominal muscles, *AB*; to muscles of back, *DO*. Inspiratory motor nerves. *PH*. Phrenic to diaphragm, *D*. *INT*. Intercostal nerves. *RL*. Recurrent laryngeal. *CX*. Pulmonary fibers of vagus that excite inspiratory center. *CX'*. Pulmonary fibers that excite expiratory center. *CX''*. Fibers of sup. laryngeal that excite expiratory center. *INH*. Fibers of sup. laryngeal that inhibit the inspiratory center. (LANDOIS.)

Such facts as those just mentioned appear to show that the pneumogastric nerve contains two sets of afferent fibers, one set (*CX*, Fig. 367) conveying impulses that excite the inspiratory center (*INS*), the other set (*CX'*), conveying impulses that excite the expiratory center (*EXP*), both sets of fibers originating in the lungs at the periphery of the pneumogastric nerves. From the fact that inflation of the lungs appears to cause expiration and collapse inspiration, and that the effects of opening the pleural cavity or of occluding the bronchus on one side are the same as the following division of one pneumogastric nerve, it is usually held at the present day that the mechanical

conditions existing at the end of inspiration and expiration constitute the stimuli to the same, the impulses then generated being transmitted by the afferent fibers to the expiratory and inspiratory centers respectively. It should be mentioned, however, that according to some physiologists at the end of expiration the accumulation of carbon dioxide in the air cells excites the afferent fibers that convey impulses to the inspiratory center and so causes inspiration.

It is doubtful, however, whether the carbon dioxide present in the lungs at the end of expiration exists in sufficient quantity to excite the fibers conveying impulses to the inspiratory center. That the pneumogastric nerves are essential to the proper performance of respiration is shown by the fact that death usually takes place after their division in an animal within from one to six days—recovery taking place occasionally however through reunion of the divided ends. Stimulation of the central ends of the superior and inferior laryngeal branches of the pneumogastric nerve diminishes or even arrests altogether respiration in the expiratory phase. The fibers of the superior laryngeal nerve are exquisitely sensitive, the functional significance of which is well illustrated by those cases in which foreign bodies entering the larynx during deglutition not only arrest inspiration but excite expiration and are coughed out. The impulses generated by the presence of foreign bodies in the larynx are conveyed to "a cough center" which appears to be situated in the medulla (Fig. 368) whence efferent impulses are transmitted to the expiratory muscles. It may be mentioned in this connection that the cough center receives impulses not only from the larynx, but also from the nose, ear, pharynx, œsophagus, and stomach.

FIG. 368.



Schema of the afferent nerves through which coughing may be excited reflexly. The efferent nerves are dotted. (LANDOIS.)

The fibers of the glosso-pharyngeal nerve also arrest inspiration, the respiratory center being inhibited through impulses generated by the passage of food during deglutition. That breathing should be suspended during an interval equal to about that of the three preceding respirations is obviously of great advantage, otherwise the

solid and liquid food would be constantly sucked into the larynx when swallowed.

Respiration may also be arrested through excitation of the sensory fibers of the olfactory, of the nasal branch of the fifth pair, of the laryngeal and pulmonary branches of the pneumogastric, of the splanchnic, and under certain circumstances of the sciatic and sensory nerves in general, though the effect of stimulation of the latter is usually to excite inspiration. On the other hand, stimulation of the cutaneous nerves increases primarily the number and depth of the respirations, though finally arresting respiration in the expiratory phase.

Every one is familiar with the fact that the dashing of cold water in the face, or the first plunge into a cold bath, and the application of a pungent vapor to the nostrils, cause involuntary respiratory efforts. It is well known, also, that the first inspiratory efforts of the newborn child are usually made in response to the stimulation of the cool external air coming in contact with the face, and that impressions on the general surface, such as a slap on the face or upon the buttocks, will frequently excite the child to breathe when otherwise it would not do so. It would appear, therefore, that impressions made upon the general sensory surface when transmitted to the medulla will cause, through stimulation of the respiratory center reflexly, inspiratory movements, as well as stimuli transmitted through the pneumogastrics.

Efferent Respiratory Nerves.

The efferent nerves involved in easy breathing are the phrenics, spinal, and pneumogastric nerves. The importance of the phrenic nerves in respiration is shown by the fact that after their division, the diaphragm, being paralyzed, is so relaxed, that it is drawn up into the thorax with each inspiration, and which interferes so with the proper expansion of the lungs that death follows from asphyxia within a few hours. On the other hand, if the spinal cord be divided at the level of the fifth cervical nerve, that is below the origin of the roots of the phrenics, though diaphragmatic breathing continues, costal respiration ceases on account of the impulses that pass normally from the respiratory center to the intercostal muscles being then cut off. If the cord be divided however above the origin of the phrenic nerves both diaphragmatic and costal breathing soon cease though respiratory movements of the larynx, face, mouth, and neck may persist. The opening of the glottis, which we have already described as accompanying synchronously inspiration, is due to impulses transmitted from the respiratory center by the fibers of the laryngeal branches of the pneumogastric nerves, particularly by those of the inferior laryngeal. If the pneumogastric be divided above the origin of its laryngeal branches through the paralysis of the muscles of the larynx the vocal membranes become flaccid, the glottis is narrowed, little or no air enters, and respiration soon

ceases. In forced breathing the spinal nerves innervating the extraordinary muscles of respiration, the facial hypo-glossal and spinal accessory nerves, are involved, as well as the nerves just mentioned. The respiratory center is not only connected with the periphery by afferent and efferent nerves but also with the cerebral cortex, as shown by the fact already mentioned that we can modify voluntarily our breathing, at least to some extent. By many physiologists respiratory centers are said to exist in the optic thalami, corpora quadrigemina, pons Varolii, and other situations, as well as in the medulla. If such centers do exist, which is extremely doubtful, they can exert only a secondary influence upon respiration.

The œsophageal branches of the pneumogastric given off both above and below the pulmonary ones unite to form the œsophageal plexus, which supplies the muscular tissue and the mucous membrane of the lower third of the œsophagus. These branches contain both sensory and motor fibers, the latter being probably more numerous, since the mucous membrane cannot be said to be acutely sensitive to heat, cold, or strong irritants.

That the motor fibers supplying the œsophagus are derived from the pneumogastric nerve can be shown by experiments like those of Bouchardat and Sandras,[1] Chauveau,[2] Longet,[3] Bernard,[4] in which, after division of the pneumogastric nerve, the œsophagus was paralyzed and distended by the food which the animal vainly endeavored to swallow. It is still a question, however, from what nerve the motor fibers of the lower third of the œsophagus are derived, since, according to Chauveau, stimulation of the bulbar roots of the spinal accessory, the most probable source, do not excite contractions of the œsophagus. The abdominal branches of the pneumogastric nerve differ somewhat in their course, according as they are distributed to the two sides. That of the left side, situated anteriorly to the cardiac opening of the stomach, immediately after passing with the œsophagus into the abdominal cavity, gives off numerous branches, some of which are distributed to the muscular walls and mucous membrane of the stomach, while others pass, in company with the sympathetic, along the course of the portal vein to the liver. That of the right side, situated posteriorly, passes through the œsophageal opening of the diaphragm, and, after sending a few filaments to the muscular coat and the mucous membrane of the stomach, is distributed to the liver, spleen, kidneys, suprarenal in company with the sympathetic capsules, the small and large intestine. The gastric branches of the pneumogastric nerves consist of motor, secretory, and probably of afferent fibers as well.

There can be no doubt, also, that stimulation of the pneumogastric nerves causes the stomach to contract, and that the movements of

[1] Comptes rendus, Tome xxiv., p. 59. Paris, 1847.
[2] Journal de la physiologie, Tome v., p. 342. Paris, 1862.
[3] Traité de Physiologie, Tome iii., p. 547. Paris, 1869.
[4] Systéme Nerveux, Tome ii., p. 422. Paris, 1858.

the stomach may to a certain extent at least, be reëstablished by stimulation of the peripheral extremities of the divided nerves. Inasmuch, however, as several seconds elapse between the application of the stimulus and the contraction, it is probable that the muscular contractions of the stomach induced by the stimulation of the pneumogastrics, are due to its sympathetic fibers, rather than to the stimulation of the nerve fibers of the pneumogastric proper, the tardiness in action just mentioned being characteristic, as we shall see, of the sympathetic. If such be the case, it would appear that the impressions due to the presence of food in the stomach are transmitted by the abdominal branches of the pneumogastric to the medulla, the efferent impulses being reflected thence to its muscular walls by sympathetic fibers.

According to some physiologists the gastric branches of the vagus contain inhibitory as well as motor fibers; the former appear however to be derived from the splanchnic nerves which we shall see hereafter pass from the sixth to the tenth thoracic ganglia to the solar plexus and thence to the stomach. As it is well known, however, that the stomach, even when entirely removed from the body, still executes movements of a normal character, it appears that the vagi regulate the movements of the stomach rather than originate them, the latter being due probably to stimuli emanating from Auerbach's plexus, situated between the muscular coats of the intestine and Meissner's plexus in the submucous coat. That the vagi contain secretory fibers is shown by the fact that direct stimulation of the nerves, proper precautions being taken, gives rise to a marked secretion of gastric juice. That the secretion can be also excited indirectly reflexly by afferent impulses transmitted from the periphery to the medulla and thence by the secretory fibers of the vagi to the stomach is shown by the following considerations. In cases of gastric fistulæ in man and animals, it has often been noticed that the placing of food in the mouth or even the sight of food, excited a copious secretion of gastric juice. This was also observed in experiments made upon dogs in which the food, after being taken into the mouth, instead of being swallowed and entering the stomach, passed by a fistulary opening in the œsophagus out of the body, the food constituting therefore only a "fictitious meal."[1] That gastric digestion is profoundly influenced by the pneumogastric nerves is further shown by the fact that if they be divided during full digestion in a living animal in which a gastric fistula has been established, so that the interior of the stomach can be examined, the muscular contractions will be observed[2] to cease instantly, the mucous membrane to become pale and flaccid, the secretion of the gastric juice to be arrested, and the organ to have become insensible.

It must be mentioned, however, that even when both pneumo-

[1] Pawlow u. Schumowa Simanowskaja, Du Bois Reymond Archiv, 1895, s. 53.
[2] Bernard, op. cit., Tome ii., p. 422.

gastric nerves are divided, if the animal survive the operation, in a day or two digestion may be partly reëstablished[1] if the food be finely divided and carefully introduced into the stomach. It is quite possible that the impression due to the presence of food in the stomach and intestines, after reaching the plexus of Meissner, situated in the submucous tissue, and the plexus of Auerbach, lying between the muscular coats is at once reflected back to the stomach without being transmitted to the medulla. Whether the reflex nervous mechanism involved in gastric digestion be such as just mentioned or not, there can be no doubt that digestion in man is very much influenced by the nervous system. Every one is familiar with the fact that digestion may be at once stopped by nervous excitement, such as a piece of bad news, etc.; that there exists an intimate sympathy between the brain and the stomach at all times, and it is difficult to understand by what avenues, other than the abdominal branches of the pneumogastric nerve, impressions are carried to and from these organs. That the abdominal branches of the pneumogastric influence also absorption from the stomach and intestinal digestion may be inferred from the fact that, after division of the pneumogastric nerves, the absorption of poisons is retarded, if not prevented, and that the most powerful cathartics fail to produce their characteristic purgative effects,[2] just as, under similar circumstances, digitalis fails to diminish the action of the heart.[3]

The branches of the pneumogastric nerves supplying the small and large intestine appear to contain motor fibers, at least stimulation of the pneumograstic nerves causes contraction of the intestine, the stimulus acting, however, as in the case of the stomach, indirectly through the plexuses of Auerbach and Meissner. According to some observers the intestinal nerves contain also inhibitory fibers. It has not yet been established, however, whether the inhibitory fibers pass to the intestine by the pneumogastric or the sympathetic, or by both nerves. In all probability the pneumogastric contains also fibers which excite the intestinal secretion, since it has been established that stimulation of the pneumogastric after a long latent period causes a flow of the secretion of the pancreas. It is said that division of the pneumogastric nerve through its abdominal branches produces, also, congestion of the liver, renders the bile watery, and arrests its glycogenic function. The production of sugar is, however, exaggerated by stimulation of the central ends of the divided nerves. The action is a reflex one, stimulation of the peripheral ends having no effect in this respect. The efferent impulses appear to be transmitted from the center, in the medulla, by the sympathetic, rather than by the pneumogastric nerve, since division of the latter between the lungs and liver does not affect the production of sugar.

[1] Schiff, Leçons sur la physiologie de la digestion, Tome ii., 389. Florence, 1867. Longet, op. cit., Tome iii., p. 549.

[2] Brodie, Phil. Trans., Vol. xiv., p. 104. London, 1814. Reid, Phys. Anat. and Path. Researches. London, 1848. Wood, American Journal of the Med. Sciences, Vol. lx., p. 75. Phila., 1870.

[3] Traube, Gesammelte Beiträge zur Path. u. Physiologie, Bd. i., s. 190. Berlin.

The Eleventh Nerve.

The spinal accessory or the eleventh nerve (Fig. 355), consisting of from 2000 to 2500 fibers arises by two distinct sets of roots—upper and lower. The upper root or the bulbar portion, originating in a nucleus lying close to the central canal, and continuous with the nucleus of the pneumogastric nerve (Fig. 337, *XI*), emerges from the side of the medulla below the latter nerve. The lower roots or the spinal portion, originating in the anterior cornu of the cord, curve backward, and, passing through the gray substance and lateral columns of the cord, emerge from the latter as six or eight filaments between the anterior and posterior roots of the first and seventh cervical nerves inclusive. The spinal accessory nerve so formed enters the cranial cavity by the foramen magnum, and leaves the latter by the jugular foramen in company with the pneumogastric and glosso-pharyngeal, and the jugular vein. During its course the spinal accessory receives from or gives off some filaments to adjacent nerves. Frequently, as it enters the cranial cavity, it receives filaments from the posterior roots of the first two cervical nerves, to which its recurrent sensibility is due; occasionally also it gives off a filament to the superior ganglion or ganglion of the root of the pneumogastric. It also receives filaments from the anterior branches of the second, third, and fourth cervical nerves. After emerging from the jugular foramen the spinal accessory gives off also two branches—internal and external—meriting special notice. The internal branch, consisting principally, if not entirely, of the fibers derived from the medulla, passes to the pneumogastric, subdividing as it joins the latter into two small branches, the first of which constitutes a part of the pharyngeal branch of the pneumogastric as already observed; the second, however, becomes so intimately united with the pneumogastric nerve that its final distribution cannot be made out by dissection alone, experiment only indicating its functional significance, as we shall see presently. The external branch of the spinal accessory, larger than the internal, and derived principally from the fibers of the spinal cord, pass through the posterior portion of the upper third of the sterno-cleido-mastoid muscle, receiving filaments in its course through the muscle from the second and third cervical nerves, to be finally distributed to the trapezius muscle.

That the spinal accessory nerve is essentially motor in function, supplying the muscles just mentioned, can be demonstrated experimentally by cutting through the occipito-atloid ligaments and stimulating the roots of the nerve within the spinal canal by electricity. If, however, the filaments arising from the medulla only be stimulated contractions of the muscles of the larynx and pharynx alone ensue, no movements of the sterno-cleido-mastoid or trapezius being observed. On the other hand, if the filaments arising from the spinal cord only be stimulated then the sterno-cleido-mastoid and

trapezius muscles alone contract, the laryngeal and pharyngeal muscles remaining quiescent. Not only does this striking experiment confirm what the distribution of the spinal accessory would lead us to suppose as to its general motor functions, but it also clearly shows that the muscles of the larynx must be supplied by the spinal accessory—that is, that the fibers of the recurrent laryngeal nerves supplying the muscles of the larynx, except the crico-thyroid, are derived not from the pneumogastric but from the spinal accessory nerve.[1] The spinal accessory nerve appears to be endowed also with a certain amount of direct, apart from the recurrent, sensibility already referred to. Whatever sensibility it does possess is, however, due undoubtedly to those filaments derived from the pneumogastric and cervical nerves. In speaking of the functions of the inferior laryngeal branches of the pneumogastric nerve it was mentioned that those nerves consisted of two kinds of fibers, one set influencing the respiratory action of the glottis, another regulating phonation, and that the latter were in reality derived from the internal branch of the spinal accessory. It only remains, therefore, to describe the manner in which this can be demonstrated, since the fibers of the inferior laryngeal nerves influencing phonation cannot be traced by dissection back to the spinal accessory. Bischoff was the first to demonstrate the influence exerted by the internal branch of the spinal accessory nerve upon the production of the voice by opening in a goat the spinal canal through the occipito-atloid space, and dividing all its roots on both sides, the result being entire extinction of the voice, whatever sound was emitted after the experiment being one which in no wise could be called voice.[2] As this method of procedure was however unsuccessful in the six preceding experiments, five of which were performed upon dogs and one upon the goat, even in the hands of such a skilful anatomist and physiologist as Prof. Bischoff, that introduced later and habitually practiced by Bernard is a far more satisfactory one. This consists in following by dissection the external or muscular branch of the spinal accessory up to the point where it emerges from the jugular foramen, and where it separates from the internal branch, and then, after seizing the combined trunk between the blades of a forceps, by steady and continuous traction to extract the whole nerve with both its medullary and spinal roots entire ; or to remove the medullary portion with the internal branch alone, leaving the spinal portion with the external branch intact, in which case the voice is entirely lost ; or to remove the spinal portion with the external branch, leaving the medullary portion with the internal branch intact, in which case the voice is unaffected or in some cases even rendered clearer.[3] It is an interesting fact that in a chimpanzee dissected by Vrolik the internal branch of the spinal accessory

[1] Bernard, Systeme Nerveux, Tome ii., p. 296.

[2] "Qui nentiquam vox appellari potuit." Bischoff, Nervi Accessorii Willisii Anatomia et Physiologie, p. 94. Darmstadii, 1832.

[3] Bernard, op. cit., Tome ii., p. 296.

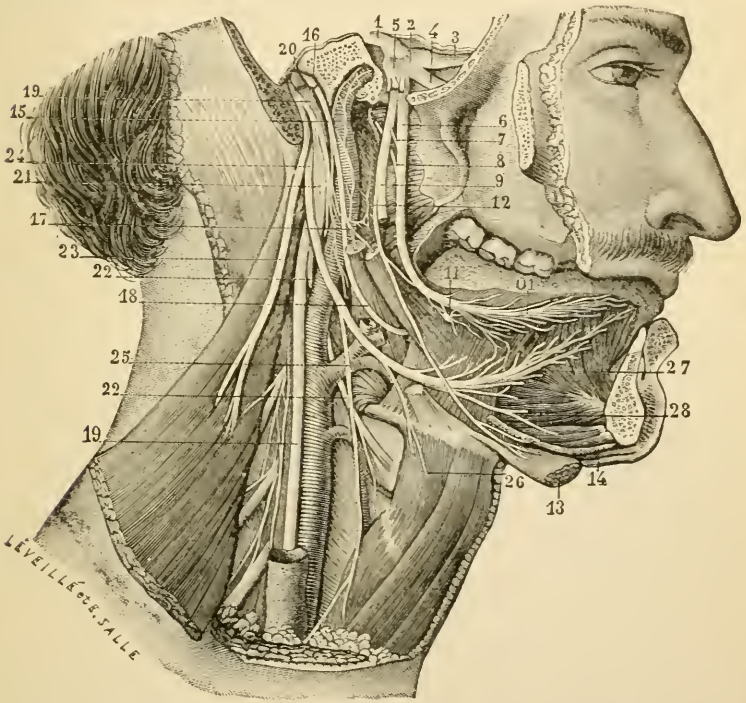
was found passing directly to the larynx instead of to the pneumogastric. The usual disposition in this anthropoid appears, however, to be the same as obtains in man, at least such was found to be the case in three individuals dissected by the author. After what has been said of the influence exerted by the pharyngeal branches of the glosso-pharyngeal and of the pharyngeal and inferior laryngeal branches of the pneumogastric in deglutition, and of the inhibitory effects upon the heart by the cardiac fibers of the latter nerve, it is only necessary here to mention again that the motor fibers involved in the performance of the above functions are derived from the internal branch of the spinal accessory; at least partly so in the case of deglutition, and entirely so in that of the inhibition of the heart. As to the function of the external or muscular branch of the spinal accessory, it would appear that its action is to excite contraction of the sterno-cleido-mastoid and trapezius muscles, synchronously with the action exerted by the internal branch upon the laryngeal and pharyngeal muscles, the harmonious action of the muscles so brought about being of advantage under certain circumstances. Thus, in prolonged vocal efforts, as in singing, for example, in which, as we shall see, the vocal membranes are put on the stretch, the upper portion of the chest is, at the same time, fixed through the action upon the shoulders, to a certain extent at least, of the sterno-cleido-mastoid and trapezius muscles, and in this way the expulsion of air through the glottis, and upon which the singing depends, can be well regulated. In the same manner, when one makes a muscular effort, the glottis is closed at the same moment that the chest is fixed, respiration being temporarily arrested. The same synchronism in the action of the external and internal branches of the spinal accessory obtain, therefore, in this instance, as in the former. That the external branches of the spinal accessory exert some influence upon the respiratory movement is well seen in animals in which the branches on both sides have been divided, such suffering from shortness of breath after any very great muscular effort, and presenting, also, irregularity in the movements of the anterior extremities, the shortness of breath being apparently due to the want of synchronous action of the sterno-cleido-mastoid and trapezius muscles.

The Twelfth Nerve.

The twelfth nerve, the hypo-glossal or sublingual, consisting of from 4500 to 5000 fibers, arises from a long column of nerve cells, the lower part of which lies in front of the central canal on each side, the upper part forming a prominence upon the floor of the fourth ventricle (Fig. 337, *XII*). Passing thence through the inner part of the olivary body, the fibers emerge as eleven or twelve filaments from the furrow between the anterior pyramid and the olivary body (Fig. 338), which, passing as two distinct bundles through two distinct openings in the dura mater into the anterior

condyloid foramen, unite into a single trunk as they emerge from the cranial cavity. Occasionally, the hypo-glossal nerve, as it passes through the foramen, receives a filament having a ganglion upon it, arising from the postero-lateral portion of the medulla. This ganglionated filament, or posterior root, so to speak, of the hypo-glossal nerve, while exceptionally present in man, is, however, found normally in the dog, cat, rabbit, hog, horse, and calf, and is sensory in function in these animals, the anterior portion of the common trunk corresponding to the hypo-glossal in man, being

FIG. 369.



Distribution of the sublingual nerve. 1. Root of the fifth nerve. 2. Ganglion of Gasser. 3, 4, 5, 6, 7, 9, 10, 12. Branches and anastomoses of the fifth nerve. 11. Submaxillary ganglion. 13. Anterior belly of the digastric muscle. 14. Section of the mylo-hyoid muscle. 15. Glosso-pharyngeal nerve. 16. Ganglion of Andersch. 17, 18. Branches of the glosso-pharyngeal nerve. 19, 19. Pneumogastric. 20, 21. Ganglia of the pneumogastric. 22, 22. Superior laryngeal branch of the pneumogastric. 23. Spinal accessory nerve. 24. Sublingual nerve. 25. Descendens noni. 26. Thyro-hyoid branch. 27. Terminal branches. 28. Two branches, one to the genio-hyo-glossus, and the other to the genio-hyoid muscle. (SAPPEY.)

motor. After the hypo-glossal passes out of the cranial cavity it gives off filaments to the sympathetic, to the pneumogastric, to the upper two cervical nerves, and to the lingual branch of the fifth. Descending behind the pneumogastric nerve (Fig. 369) it curves downward and forward to the outer side of the latter, between the internal carotid artery and the jugular vein, and penetrates the genio-hyo-glossal muscle, which it supplies, as also the hyo-glossus, lingualis, genio-hyoid, and stylo-glossus muscles.

The hypo-glossal gives off, also, an important branch, the descendens noni, but which, according to the classification of the nerves usually adopted, would be more correctly called the descending branch of the twelfth, supplying the sterno-thyroid, sterno-hyoid, and omo-hyoid muscles, the thyro-hyoid muscle being supplied by the branch of the same name. From the distribution of the hypo-glossal nerve it might naturally be inferred that it is essentially motor in function, any sensibility that it possesses being due to the filaments communicating with the cervical and pneumogastric nerves, and the lingual branch of the fifth. That such is the case is shown by the effect of division of the hypo-glossal in a living animal, and of its paralysis in man. Under such circumstances, through paralysis of the tongue, though the tactile and gustatory senses are not affected, mastication is rendered very difficult, if not impossible, while, through paralysis of the muscles depressing the larynx and hyoid bone, deglutition is made difficult; in man the power of articulation is lost as well. This is well seen in cases of glosso-labio-laryngeal paralysis, in which the nuclei of origin in the medulla of the hypo-glossal, as well as the facial, spinal accessory, and glosso-pharyngeal nerves are affected by disease, which involves a gradual and progressive paralysis of the tongue, palate, lips, and laryngeal muscles, rendering articulation, and ultimately deglutition, impossible.

In cases of hemiplegia the hypo-glossal nerve is usually more or less involved. In such cases the patient protrudes the tongue, the point being deviated to the side affected with the paralysis, owing to the unopposed action of the genio-hyo-glossus muscle of the sound side. That the hypo-glossal nerve is a motor nerve—the motor nerve of the tongue, etc.—is further shown by the effect of stimulating the peripheral end of the divided nerve, the tongue, and the muscles to which the nerve is distributed at once contracting. The hypo-glossal nerve, together with the small or motor root of the fifth and the facial nerves, constitutes the efferent fibers, by which the reflex action involved in mastication is accomplished, the lingual branch of the fifth and the glosso-pharyngeal nerves, containing the afferent fibers, the center being situated in the medulla.

Having described the distribution and function of the ten pairs of cranio-medullary nerves, and having seen that they arise from gray nuclei in the medulla oblongata, it is evident that the medulla consists, not only as we have seen, of fibers passing from the cord to the ganglion of the base of the brain, but may be regarded, also, as being composed of so many distinct reflex centers, of which the cranio-medullary and spinal nerves constitute the afferent and efferent fibers; the existence in the medulla of about fourteen such centers, probably more, has been established. First. That for closing the eyelids, the efferent fibers being contained in the optic nerve, and the branches of the fifth distributed to the conjunctiva and to the skin of the lids, the efferent fibers in the facial. Second. The

center for sneezing, the afferent fibers, being in the olfactory and the fifth nerve, the efferent in the spinal nerves influencing expiration. Third. The center for coughing, the afferent fibers rising in the pneumogastric, the efferent being the same as those last mentioned. Fourth. The respiratory center, or nœud-vital of Flourens. Fifth. The masticatory center. Sixth. The center of insalivation. Seventh. The center of deglutition. Eighth. The cardio-inhibitory centers, the afferent and efferent fibers of which have already been referred to. Ninth. The center for sucking, the afferent fibers of which are in the fifth and glosso-pharyngeal nerves, the efferent the facial supplying the lips. Tenth. The center influencing the act of vomiting, the afferent fibers being in the pneumogastric, the efferent in the nerves of expiration. Eleventh. The center of speech—that is, with reference to the movements of the lips, tongue, and larynx. Twelfth. The vasomotor center. Thirteenth. The center inhibiting the reflex centers of the spinal cord.

The medulla oblongata being the seat of the centers receiving the afferent fibers and giving off the efferent ones involved in the performance of mastication, insalivation, deglutition, respiration, circulation, etc., is, therefore, the great coördinating center of the reflex actions essential to the maintenance of life. Even if all the parts of the brain above the medulla be removed in a living animal, or be undeveloped, as in anencephalous infants, life may yet be maintained by artificial means, since, if food be introduced into the mouth it will be swallowed, the respiratory and circulatory movements will go on in the usual rhythmical manner, the animal or infant will react to impressions made upon the general sensory surface, withdrawing its limbs, etc., if pulled or pinched, may even utter a cry, as if in pain, and yet such an animal or human being cannot be said to be really a sentient, still less an intelligent, being, but merely a nutritive reflex mechanism.

CHAPTER XXXIII.

THE NERVOUS SYSTEM.—(*Continued.*)

THE PONS VAROLII. CRURI CEREBRI. CORPORA STRIATA. THALAMI OPTICI. CORPORA QUADRIGEMINA. CEREBELLUM.

Whether reflex action of the spinal cord or medulla be accompanied or not in the lower animals with sensation, volition, consciousness, there can be no doubt that the physical seat of what we call feeling, thinking, etc., in man is situated in some part of the brain above the level of the medulla oblongata, since in the absence of such parts one neither feels, thinks, nor wills. Pons Varolii. Just as we have seen that the spinal cord and medulla consist of nervous centers as well as of fibers passing through them to the ganglia at the base of the brain, so the pons Varolii or mesencephalon (Fig. 370, 1) may be regarded as consisting, not only of ascending sensory

Fig. 370.

Diagram of human brain in transverse vertical section. 1. Tuber annulare. 2, 2. Crura cerebral. 3, 3. Internal capsule. 4, 4. Corona radiata. 5, 6. Cerebral ganglia. 7. Corpus callosum. (Dalton.)

and descending motor fibers connecting the cortex with the cord, and of bridging fibers connecting the lateral lobes of the cerebellum —hence its name—but of gray matter performing the functions of a distinct nervous center or centers. That the gray matter or tuber annulare (Fig. 370, 1) is the essential part of the pons

Varolii is shown by the fact of the bridging fibers of the pons being absent in animals in which the lateral lobes of the cerebellum are undeveloped as in birds. That the tuber annulare, or vesicular matter of the pons Varolii, is that part of the encephalon in the lower mammals in which consciousness first awakens in response to impressions transmitted by the spinal and cranial nerves from the external world appears probable from experiments, such as those of Longet,[1] Vulpian,[2] etc., in which, after removal of the whole encephalon except the pons, medulla, and cerebellum, sensibility to pain still persisted, the cries emitted by an animal so mutilated not being simply reflex in character, such as are heard in an animal possessing only the medulla already referred to, but as indicating the perception of painful impressions. While it is true that the appreciation of painful and other impressions is not acute, but obscure, nevertheless that such an animal is conscious to a certain extent at least, there appears to be little doubt, their condition being apparently similar to patients undergoing a severe surgical operation, but imperfectly under the influence of an anæsthetic, and who, while undoubtedly suffering pain at the time, have no recollection of it, the impressions due to the operation not being conveyed to the cerebral hemispheres, and therefore not memorized.

Even admitting however that the physical seat of incipient consciousness lies, in the lower mammals, in the pons, there is little reason to suppose that the same part of the encephalon in man possesses such a function. Lesions of the pons, at least in man, appear to show that its function is rather of a commissural than of a psychical character.

Crura Cerebri.

It has already been mentioned that the motor tract beginning in the cortex of one hemisphere is continued downward through the anterior or inferior portion of the crus cerebri (crusta) to the decussating fibers of the medulla, and thence to the antero-lateral columns of the opposite side of the cord; that the sensory tract beginning on the opposite side of the body crosses the middle line, is continued upward through the medulla and posterior or superior portion of the crus cerebri (tegmentum) to terminate in the cortex of the same side. Such being the case, as might be anticipated if both crura (Fig. 371, 2, 2) are completely divided, sensation and voluntary movement are entirely annihilated throughout the body, division of one of the crura involving paralysis of sensation and motion on the opposite side of the body only. The constant tendency to turn toward the side opposite that of the lesion, the "evolution du manege" of Longet, observed when one crus is imperfectly divided appears to be due to the balance of the muscular action being destroyed through the weakening of the sensori motor apparatus of the opposite side. Division of the crus cerebri involves also paralysis of the oculo-

[1] Physiologie, Tome iii., p. 396. [2] Systeme Nerveux, p. 542. Paris, 1866.

motorius of the same side, and partial paralysis of the facial nerve of the opposite side, and is also followed by contraction of the arteries, a rise in blood pressure, and the loss of power to influence voluntarily the action of the sphincter ani, and the constrictor urethræ. In addition to the motor and sensory fibers just referred to, the crura cerebri contain also fibers passing from the gray matter of the medulla and pons to the hemispheres, and of fibers passing forward and backward from the locus niger, or the gray matter separating the crusta from the tegmentum, to the cerebellum, and of fibers passing from the corpora quadrigemina to the cerebellum. The functions of these fibers, so far as known, appear to be commissural in character.

Corpora Striata and Thalami Optici.

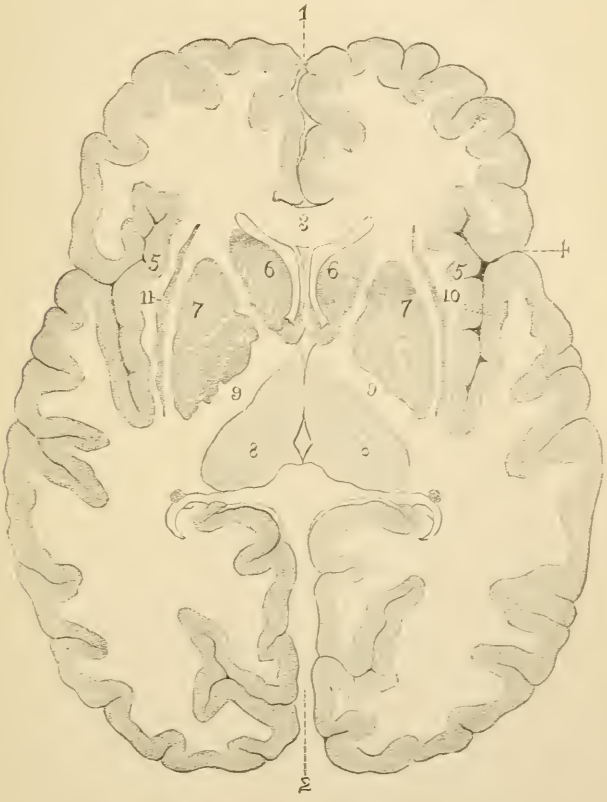
If the hemispheres of the brain be removed to the level of the corpus callosum, or the bridge of white substance uniting the cerebral hemispheres, and the former be divided and turned aside, the lateral ventricles will be exposed—that is, the two cavities having for their roof the corpus callosum, their floor the fornix, their inner walls the septum lucidum with its enclosed fifth ventricle, their outer walls the corpora striata.

Each corpus striatum, so called from presenting a striated appearance on section, projects as a half pyriform prominence into the lateral ventricle, constituting, as just said, its outer wall, the largest anterior portion being known as the head; the narrowest posterior portion the tail, the latter curving backward to the outer side of the thalamus opticus.

Each corpus striatum (Fig. 371) consists of two parts, the intraventricular, or nucleus caudatus (6), and the extraventricular, or nucleus lenticulares (7). The latter consists of three parts separated by white matter, the striæ medullares; the two inner central parts being called the globus pallidus, on account of their pale color, the outer external part the putamen. The caudate and lenticular nuclei are separated by the internal capsule (9) or the diverging fibers of the crus cerebri, to which the corpus striatum owes its name, the external capsule (10) with the claustrum (11) lying to the outer side of the nucleus lenticularis and close to the insula or island of Reil (5). If now the fornix or floor of the lateral ventricle be removed, a narrow triangular cavity will be exposed, the third ventricle, communicating, on the one hand, with the lateral ventricles by the foramina of Monro, and on the other with the fourth ventricle by the iter, the latter passing under the corpora quadrigemina, to be mentioned presently. The floor of the third ventricle is formed from before backward by the optic commissure, infundibulum, mammillary eminences, posterior perforated space, and cerebral crura; its walls by the thalami optici, situated on the inner side of the crura cerebri, and separated from the corpora striata by the internal capsule and tænia semicircularis.

Each thalamus opticus consists internally of white matter, externally of both white and gray matter. The most prominent parts of the thalamus opticus anteriorly, are known as its tubercles, posteriorly as the pulvinar. Beneath the latter are situated the corpora geniculata from which arise partially the optic tracts.

FIG. 371.



Horizontal section of the hemispheres at the level of the cerebral ganglia. 1. Great longitudinal fissure, between frontal lobes. 2. Great longitudinal fissure, between occipital lobes. 3. Anterior part of corpus callosum. 4. Fissure of Sylvius. 5. Convolutions of the insula. 6. Caudate nucleus of corpus striatum. 7. Lenticular nucleus of corpus striatum. 8. Optic thalamus. 9. Internal capsule. 10. External capsule. 11. Claustrum. (DALTON.)

One of the best established facts in human or animal cerebral pathology is that a destructive lesion of the corpus striatum, whether produced by disease or experimentally, is followed by a paralysis of motion of the opposite side of the body, sensation remained unimpaired. It is true that in some exceptional cases the paralysis is on the same side of the body, but there is no question in such cases as to the paralysis due to the lesion of the corpus striatum being that of motion.

It has also been shown that electrical stimulation of the corpus

striatum in a living animal, monkeys, dogs, cats, etc., causes a general unilateral contraction of the muscles of the opposite side of the body, the latter being thrown into a condition of pleurosthotonus, in which it is bent to the opposite side, the flexor muscles being contracted apparently more than the extensor ones. It is well known also, that in the cetacea—the whale, dolphin—the elephant, etc., very muscular animals, the corpora striata are not only absolutely but relatively large and well developed. The facts of pathology, experiment, and comparative anatomy, confirm, therefore, the view based upon their anatomy that the function of the corpora striata is essentially motor.

It has been equally well established, however, that in man, unless the disorganization of the corpus striatum giving rise to hemiplegia is situated in the internal capsule the loss of voluntary motion is not persistent. It is obvious, therefore, that the axis-cylinders originating in the motor areas of the cortex, traverse, as already mentioned, the internal capsule and that disease of the corpus striatum causes permanent paralysis of motion only so far as it involves the internal capsule. Whatever, therefore, may be the functions of the corpora striata in the lower animals, these ganglia can only be said to have a motor function in the sense that they are traversed by the motor tracts from the cortex.

While lesions of the thalami optici are not of infrequent occurrence in man, from the fact that the corpora striata and adjacent parts of the hemispheres are usually involved, conclusions as to the functions of these ganglia, based upon the loss of sensibility, etc., following their destruction, cannot be accepted with the same confidence as in the case of the corpora striata. Nevertheless, if the lesion be limited, as is sometimes the case, to the corpus striatum and the thalamus opticus, and the destruction of these two ganglia is followed by loss of motion and of sensibility on the opposite side of the body, and if it be admitted that the function of the corpus striatum is motor, the conclusion that the thalamus opticus is sensory in function becomes then unavoidable. Indeed, it could not be otherwise, since after destruction of the thalamus opticus no other avenue is left by which sensory impressions can be transmitted from the general periphery of the body to the cerebral hemispheres, except by the posterior third of the posterior segment of the internal capsule or the "sensory crossway." That the thalamus opticus has some sensory function appears to be shown by the fact of its destruction in man being followed by loss of general and special sensibility on the opposite side of the body, tactile sensation being impaired, and hearing and vision in some cases affected.[1]

It might be urged, however, that in the case of man whatever sensory functions the thalami optici may be endowed with are only due to some of the axis-cylinders of the sensory tract simply travers-

[1] Luys, Recherches sur le Systeme Nerveux, 1865, p. 538. Crichton Browne, West Riding Asylum Reports, Vol. v., p. 227, 1876. Ferrier, op. cit., p. 239.

ing it to terminate in the sensory area of the cortex. That the paralysis of motion and sensation following lesions of the corpora striata and thalami optici is not due simply to the motor and sensory impulses being normally transmitted through these ganglia from or to the convolutions of the hemispheres, and that after the destruction of these ganglia no avenues are left, therefore, for the transmission of such impulses, is shown by the fact that after removal of the cerebral convolutions in a mammal the power of voluntary movement and sensation remains. Thus, for example, in a rabbit the cerebral hemispheres having been removed, while there is nothing observed to indicate that its sensations ever give rise to ideas—that is, that it perceives—nevertheless, it feels even it does not think; it sees, hears; if pinched, it cries; when stirred up, it runs or leaps forward, avoiding with more or less success obstacles placed in its path. The animal has undoubtedly possession of its senses, can execute all its bodily movements, but its intelligence appears to be gone, at least objects which would have ordinarily pleased or terrified it make no impression whatever upon it. It must be borne in mind, however, that in any application to be made of such results with the view of elucidating the functions of the basal ganglia in man, that it does not necessarily follow that a human being, or even a dog deprived of its cerebral hemispheres, should be in exactly the same mental condition as a rabbit under similar circumstances. On the contrary, there is a good reason for supposing that, as we pass from the lower to the higher mammals, the seat of voluntary motion and sensation is removed to higher and higher levels in the encephalon; the cerebral convolutions being more important in this respect in man than in a dog, and the basal ganglia more important in the dog than in the rabbit, and so on. The most marked contrast in this respect is presented by fishes,[1] in which the corpora striata are relatively well developed, the cerebral hemispheres but little so—in fact, the latter are only represented, more particularly in the cartilaginous fishes, by the thin film of nervous matter covering in the cavity or ventricle, of which the corpora striata constitute the floor; the so-called optic lobes in fishes representing, probably not only the optic lobes of the higher vertebrates, but the thalami optici as well. Undoubtedly a rabbit can do more without its basal ganglia and cerebral convolutions than a dog, and a dog with its basal ganglia but without its hemispheres than a man without the latter. It becomes, therefore, a very difficult matter to say just where sensation begins in man, and still more, where sensation is accompanied or gives rise to ideation and volition.

It has been suggested that if an impression made upon the periphery must be transmitted to the cerebral convolutions to be thoroughly appreciated, and that a voluntary impulse developed in response to such a sensation must emanate in the same, the connections of the basal ganglia through the corona radiata, with the convolu-

[1] L. Edinger, Vorlesungen über Den Bau Der Nervösen Centralorgane, 1896, s. 72.

tions of the hemispheres, and with each other, offer an avenue for the performance of reflex actions already referred to, which originally being accompanied with both sensation and volition, in time come to be performed without either. For with the constant repetition of a particular action involving sensation and volition, it is natural to suppose that the circuit traversed might become shorter and shorter, and that impressions which originally reached the cerebral hemisphere before being reflected back, simply passing through the basal ganglia to and fro, gradually take a shorter course, and reaching the thalamus opticus are at once reflected back through the corpus striatum, short-circuted, so to speak.

Optic Lobes.

It has already been mentioned that the iter or way by which the third and fourth ventricles communicate with each other, passes underneath the corpora quadrigemina. The latter consist of a white quadrate mass more or less divided upon its upper surface by a crucial depression into four eminences, the so-called nates and testes, optic lobes, or quadrigeminal bodies, whence their name. The corpora quadrigemina, or the optic lobes, as we shall hereafter for brevity designate them, are attached laterally to the thalami optici between which they are situated, and also to the geniculate bodies, and therefore indirectly with the optic tracts. Inferiorly they are connected with the cerebellum by the superior peduncles between which is attached the valve of Vieussens and with the motor columns of the cord by the fibers descending through the pons and embracing the olivary body. The optic lobes are not, however, in man, as their name would imply, the seat of the centers of vision, since the visual path, as we shall see presently, is continued as that part of the optic tract that passes beyond the optic lobes through the posterior limb of the internal capsule as the optic expansion or radiation to the cuneus in the occipital lobe. On the other hand, as in many mammals, the occipital lobe is undeveloped, the cerebellum being entirely uncovered, it is obvious that the center of vision must be situated in such mammals at least in some other part of the brain than the cuneus, the latter being absent. As a further proof that the center of vision is not situated in all animals in the same part of the brain, it may be mentioned, as we shall see presently, that the sense of sight persists in the lower vertebrata even after the entire removal of the cerebral hemisphere. The optic lobe, as might be expected, constitutes also an important part of the reflex mechanism by which the coördination of the eyeballs and the contraction of the pupil are effected, the optic nerve being the afferent nerve and the oculo-motorius the efferent nerve, the reflex centers being situated either in the optic lobe or immediately beneath it. Apart from the anatomical fact that the optic lobes are connected with the motor tracts of the spinal cord, which would, as already remarked, indicate that these

ganglia influence muscular action in some way, it is well known that the optic lobes are not invariably developed in proportion to the eyes, but, on the contrary, may be quite large, though the eyes and optic tracts be but small, little developed, or even wanting altogether, as, for example, in the myxine or hag fish, and the Apterichthys cæcus among fishes, in the proteus and cecilia among batrachians, and in moles and shrews among mammals, which show that the optic lobes have other functions beside those influencing vision. Now, while it has been established that destruction of the optic lobes in animals involves disorders of equilibrium and want of muscular coördination, nevertheless, it must be mentioned that a very great difference prevails in this respect according to whether the animal upon which the experiment is performed be a batrachian, bird, or mammal, the optic lobes relatively to the cerebral hemispheres being so much better developed in the lower than in the higher vertebrates. Thus, for example, a frog with its optic lobes intact, but without its cerebral hemispheres, can coördinate its muscles for the performance of ordinary actions better than a pigeon or a rabbit similarly conditioned, and the latter better than a monkey or man. It may be mentioned, also, in this connection, that the want of coördinating power, etc., following destruction of the optic lobes is not due, as might be supposed, to the blindness entailed, since in the frog, for example, if the eyes be destroyed, but the optic lobes be left intact, such disorders as those ensuing upon the destruction of these ganglia are not observed. It is well known that if all the encephalic centers above the optic lobes be removed in the frog, gentle stroking of the back excites the animal to croak. The croaking entirely ceasing, however, if the optic lobes be removed, the natural inference is that these ganglia contain the reflex centers through which the croaking is produced. As certain plaintive cries emitted by the rabbits cease after removal of the optic lobes, it is possible that a similar reflex center exists in the optic lobes of mammals as well as in those of frogs.

Taking this latter fact into consideration, together with that of the circulation and respiration being modified by electrical stimulation of the optic lobes, the blood pressure being increased, the heart slowed, the respiration deepened exactly in the same manner as when the sensory nerves are powerfully excited, and that contractions of the stomach, intestines, and bladder also follow, it would appear that the optic lobes influence nutrition as well as muscular coördination and vision.

The Cerebellum.

The cerebellum, constituting about one-eighth of the bulk of the brain, and situated in the posterior fossæ of the cranial cavity, consists of two lateral portions, the hemispheres, the anterior rounded eminences of which are known as the amygdalæ, or the tonsils. The hemispheres, though separated behind and below by

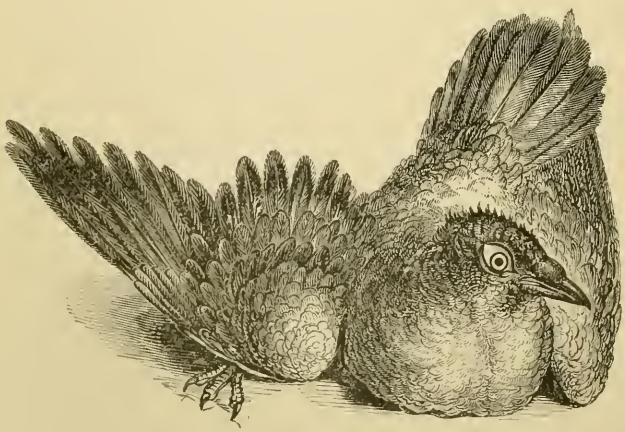
a wide deep groove, the vallecula or valley, are connected by an intermediate worm-like ridge, the vermiform process, the portion of the latter situated between the tonsils being called the uvula, while just above the tonsils, and separated from them by a fissure, may be seen the flocculi, or pneumogastric lobules, so called from their vicinity to the nerve of the same name. Each lateral hemisphere and vermiform process essentially consists internally of a prismoid trunk of white substance, from which emanate about a dozen broad, thin laminæ; the latter subdividing again into secondary thinner laminæ, and the gray substance enfolding them, gives rise to the convolutions and fissures observable on the surface of the organ.

It has already been mentioned incidentally that the optic lobes are connected posteriorly with the cerebellum through the superior peduncles of the latter. The fibers of the superior peduncles passing forward and upward to the testes ascend through the crura cerebri to the thalamus opticus and corona radiata, and thence to the frontal temporal and occipital lobes, some of the fibers decussating beneath the optic lobes. Inferiorly the superior peduncles are connected with the vermiform process of the cerebellum and with the corpus dentatum, or punch-like layer of gray matter within the white matter of the lateral hemispheres. The middle peduncles of the cerebellum constituting, as already mentioned, the transverse commissural fibers of the pons Varolii connect the two lateral hemispheres, while the inferior peduncles pass downward into the restiform bodies of the medulla, and are collected with the spinal cord.

According to most histologists each lateral lobe of the cerebellum is connected with the olivary body of the opposite side, the tract constituting the so-called "cerebro-olivary" system.

If the cerebellum be removed in a bird, a pigeon, for example (Fig. 372), though the animal still feels, thinks, wills, it is unable

FIG. 372.



Pigeon, after removal of the cerebellum. (DALTON.)

to stand or fly. If placed upon the back, it is unable to rise. If food be placed within its reach, though it sees it, it cannot pick up the food. Instead of remaining quiet, it is in a continual state of restlessness and agitation. In a word, though able to make voluntary movement, the animal has lost the power of coördinating its movements for the performance of a definite object, or of maintaining its equilibrium. Its movements highly resemble those of a drunken man. Essentially the same results are obtained if the cerebellum be removed in a mammal. Undoubtedly then, very remarkable disorders, both as regards the maintenance of equilibrium and power of locomotion ensue upon destruction of the cerebellum in mammals and birds, although, as already mentioned, no perceptible change is observable in these respects in the case of frogs, in which the cerebellum has been removed.

Differences of opinion still prevail among pathologists as to whether lesions of the cerebellum in man give rise to the same disorders as observed in mammals and birds, in which the cerebellum has been removed, and even though it has been held by some physiologists that entire absence of the cerebellum, as shown by post-mortem examinations, was not accompanied during life with loss of the power of locomotion, or of the maintenance of equilibrium, nevertheless, it may be questioned whether there is a well-authenticated case in which locomotion and equilibrium remained unaffected, extensive lesions of the cerebellum existing. Such cases as where there was a congenital absence of the cerebellum, unaccompanied with any disorders of locomotion, etc., being explainable on the supposition that, as in the case of the frog, the function of the cerebellum was performed by other ganglia, probably the optic lobes. On the supposition that the cerebellum is the center for the maintenance of equilibrium and of muscular coördination, it ought to be best developed in those animals which exhibit such powers in a marked degree, and such we find to be the case. Thus in the shark, for example, in which, of all fish, the muscular system is best developed, and the power of coördination so perfect, as shown, for example, in the manner in which it seizes its prey, the cerebellum is larger and more complex in its structure than in any other fish. Among birds, also, the cerebellum is particularly well developed in the carnivorous raptores, in which muscular actions, such as are involved in the swooping down by them upon prey from immense heights, require very nice adjustment of coördination. Among mammals the cerebellum is large; in the kangaroo, whose peculiar mode of progression necessitates considerable muscular coördination, while, in the elephant, in which great muscular coördination is demanded, owing to the enormous muscular development, and in the case of the posterior extremities to the absence of the round ligament of the hip-joint, the cerebellum is very large, being equal to one of the hemispheres. In the anthropoid apes, also, which not unfrequently assume the semi-erect attitude, the cerebel-

lum is larger than in the remaining monkeys. Indeed, in the young chimpanzees and orangs dissected by the author[1] the cerebellum was found so well developed as to extend slightly beyond the posterior lobes of the cerebrum, which is not the case in monkeys generally, in adult chimpanzees or orangs and in baboons, macaeques, spider-monkeys, etc., the cerebellum being perfectly covered by the posterior lobes of the cerebrum as in man. That the cerebellum, at least in mammals, birds, and fishes, is concerned in some way in the maintenance of equilibrium and muscular coördination is not only shown by experiment, pathology, and comparative anatomy, but from the fact of the tactile, visual, labyrinthine, and perhaps visceral impressions upon which the maintenance of equilibrium and muscular coördination depend, being transmitted from the periphery through nerves which directly or indirectly terminate in the cerebellum, as we shall now endeavor to show. It has already been mentioned that a frog from which the cerebral hemispheres have been removed, but which still preserves its optic lobes and cerebellum, retains the power of maintaining its equilibrium and of muscular coördination. If, however, the skin be removed from the hinder legs of such a frog, the animal at once loses this power and falls like a log if the position of its support be changed, the removal of the skin making impossible the transmission of those afferent tactile impressions which through some reflex center give rise to those efferent muscular actions requisite for the maintenance of equilibrium. That this reflex center is situated in man in the cerebellum, and that these afferent tactile impressions are transmitted by the posterior columns of the spinal cord, is rendered very probable from the fact that sclerosis of these columns causes locomotor ataxia, a disease especially characterized not by a loss of sensibility but of power of coördination, and that the posterior columns of the cord through the restiform bodies of the medulla terminate in the cerebellum. While visual are not as important as either tactile or labyrinthine impressions in the maintenance of equilibrium, since the latter almost suffice in the absence of the former, nevertheless they exercise a certain amount of influence. Thus, in cases of locomotor ataxia, for example, equilibrium and coördination are not altogether impossible, even though the tactile impressions be wanting, so long as the labyrinthine and visual impressions persist, and in such cases when the transmission of tactile and labyrinthine impressions are perfect, the absence of visual ones always entails some slight want in the coördinating power. That such visual impressions are transmitted to the cerebellum, is rendered very probable when it is remembered that the optic lobes are connected with the cerebellum both through the superior peduncles and valve of Vieussens. As is well known, remarkable disturbances of equilibrium ensue if the membranous semicircular canals of the internal ear be divided in a bird or mammal, or if they are

[1] H. C. Chapman, Proc. Acad. of Nat. Sciences, 1879, p. 68; 1880, p. 172.

diseased as in Ménière's disease in man, which vary according to the seat of the lesion. Thus, if the horizontal canals be divided in a pigeon, for example, rapid movements of the head in a horizontal plane, from side to side, follow, with oscillation of the eyeballs, and a tendency to spin around on a vertical axis is manifested.

If, however, the posterior or inferior vertical canals be divided, the head is moved rapidly backward and forward, and the animal tends to turn somersaults backward head over heels, whereas if the superior vertical canals be divided, the head is moved rapidly forward and backward, and the animal tends to make forward somersaults heels over head. It would appear from the researches of Goltz,[1] Mach,[2] Brewer,[3] and Crum Brown[4] among others, that the character of the impressions made upon the vestibular nerves depends upon the degree and relative variations in the pressure exerted by the endolymph upon the ampullæ of the membranous canals, to which, as we shall see hereafter, these nerves are distributed. Such being the case, it is obvious that if the semicircular canals be divided disturbances of equilibrium must ensue, the natural tension of the endolymph being thereby altered, which will vary according to the particular semicircular canal affected. It may be mentioned in this connection, that pigeons in which the semicircular canals have been divided on one side in time regain the power of maintaining their equilibrium, but if the canals be divided on both sides, they never again are able to assume their natural position, the most strange and bizarre attitudes being taken. Whatever may be the nature and mechanism of the labyrinthine impressions, there can be no doubt as to the influence exerted by them in the maintenance of equilibrium, since in their absence the same becomes impossible even though the tactile and visual impressions persist. That the membranous semicircular canals and the auditory nerve together constitute an afferent system by which impressions are transmitted to the cerebellum, acting as a reflex coördinating center, appears highly probable when it is remembered that division of the auditory nerve entails disturbances of equilibrium, that the auditory nerve through the restiform bodies is directly connected with the cerebellum, and that a great similarity exists between the effects of destruction of the cerebellum and division of the semicircular canals. Thus, destruction of the anterior portion of the middle lobe of the cerebellum, like that of the superior vertical canal, involves displacement of equilibrium forward around a horizontal axis, destruction of the posterior part of the median lobe like that of the posterior vertical canal, displacement backward around a horizontal axis, destruction of the lateral lobes of the cerebellum, like that of the horizontal canals, lateral displacement around a vertical axis. The cerebellum appears, therefore, to be the reflex center by which the afferent impressions transmitted by

[1] Pflüger's Archiv, 1870. [2] Sitz. ü. der K. Acad. der Wiss., Wien, 1873.
[3] Med. Jahrbucher, Heft i., 1874. [4] Journal of Anat. and Phys., May, 1874.

the cutaneous, optic, and acoustic nerves are coördinated with the efferent ones for the maintenance of equilibrium and locomotion. That such reflex actions are accompanied now, or originally at least, with consciousness, and that the cerebellum is that part of the encephalon in which the ideas of space are developed, is rendered very probable when it is remembered that many actions involving muscular coördination, which are performed now unconsciously, were originally accompanied by both sensation and volition, and that the disorders of equilibrium and locomotion following destruction of the cerebellum or of the afferent system leading to it, imply a perversion in the ideas of space relations.

From the fact that the loss of coördinating power, etc., following division of the cerebellum in the middle line is only transitory it is usually held that each half of the cerebellum is associated with the medulla and cord of the corresponding side of the body. The relation of the cerebellum to the cerebrum however is a crossed one, each cerebellar hemisphere being connected with the cerebral hemisphere of the opposite side of the body. It appears also that the tracts connecting the cerebellum with the medulla, etc., on the one hand, and with the cerebrum on the other, constitute double pathways, the cerebellum sending as well as receiving impulses to and from the different regions with which it is associated.

CHAPTER XXXIV.

THE NERVOUS SYSTEM.—(*Continued.*)

THE CEREBRAL HEMISPHERES.

The cerebral hemispheres, so called on account of their hemispherical form, are two ovoidal masses flattened at their mesial surface, where they are separated by the great longitudinal fissure. They consist of gray or vascular and of white or fibrous nervous tissue. The gray substance, like that of the cerebellum, situated externally and varying between two and three millimeters in thickness, sinks at intervals into the white substance to a depth of from ten to twenty-five millimeters, invaginating itself—that is, folds inward to return upon itself again, and so gives rise to the convoluted and fissured surface so characteristic of the brain of man and of many mammals. It is evident that through this convoluted arrangement the hemispheres contain far more gray matter than if they were smooth, on the same principle that a pocket handkerchief occupies much less room when folded up than when laid out smooth, and that the deeper and more numerous the fissures the greater the amount of gray matter present. The gray matter of the convolution or cortical layer of the hemispheres, consists of a granular matrix in which are imbedded nerve-cells with their axons, disposed in four or more layers (Fig. 373), the latter being distinguished by the character of their nerve cells.

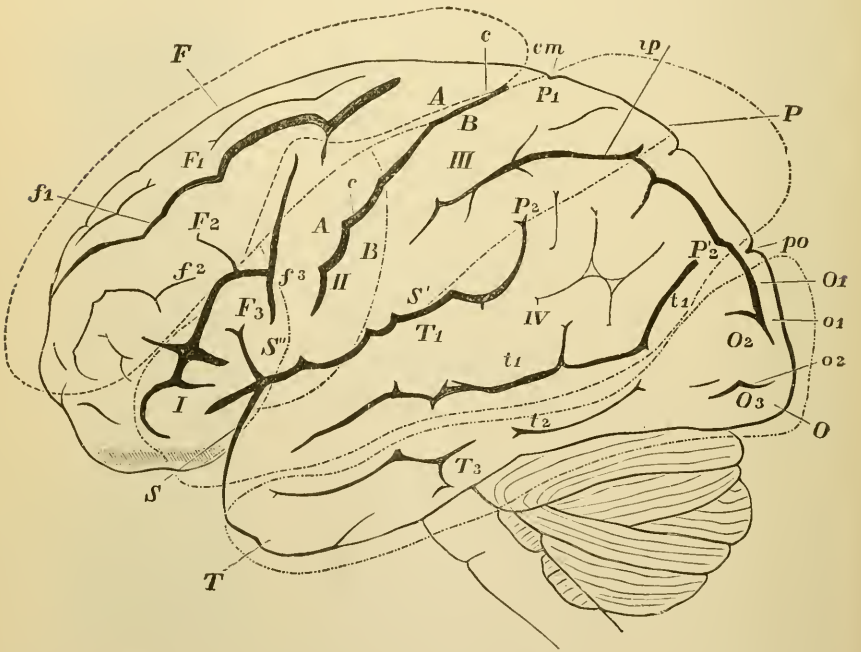
Fig. 373.

Section of a cerebral convolution stained by Golgi's method. 1. Neuroglia layer. 2. Layer of small cells. 3. Layer of large pyramidal cells. 4. Layer of irregular cells. (Landois.)

Among the most striking of these cells may be mentioned the so-called pyramidal cells, varying in diameter from the $\frac{1}{100}$ to $\frac{1}{25}$ of a millimeter ($\frac{1}{2500}$ to $\frac{1}{625}$ of an inch), and characterized by their quadrangular base and tail-like extremity, the latter pointing outwardly. The pyramidal cells are more numerous and larger in the anterior portion of the hemispheres in the convolutions of the frontal lobe, for example, the cells of the so-called nuclear layer in the occipital and temporal lobes. Certain so-called giant pyramidal cells, attaining a diameter of from the $\frac{1}{20}$ to the $\frac{1}{10}$ of a millimeter ($\frac{1}{500}$ to $\frac{1}{250}$ of an inch), probably motor in function, like those of the anterior cornu of the spinal cord, are

also found more particularly in the posterior portion of the frontal lobe in the anterior central convolution, the processes of which appear to be prolonged downward as the axons traversing the antero-lateral columns of the spinal cord and which we have seen are in relation with the anterior roots of the spinal nerves, while other cells, having no processes or axons, are found more especially in the posterior part of the hemispheres in the occipital lobe. Although the convolutions or gyri and the fissures or sulci do not run in exactly the same manner in different brains, and are not symmetrically disposed even in the two hemispheres of the same brain, nevertheless the general disposition is so constantly the same that the most important of them can be readily recognized and identified, and on account of their supposed functional importance demand at least a brief description. The most striking fissure observable, if the hemisphere be viewed laterally, both on account of its depth and constancy, it existing not only in man but in all animals whose brain is fissured at all, is the fissure of Sylvius. Beginning as a transverse

FIG. 374.

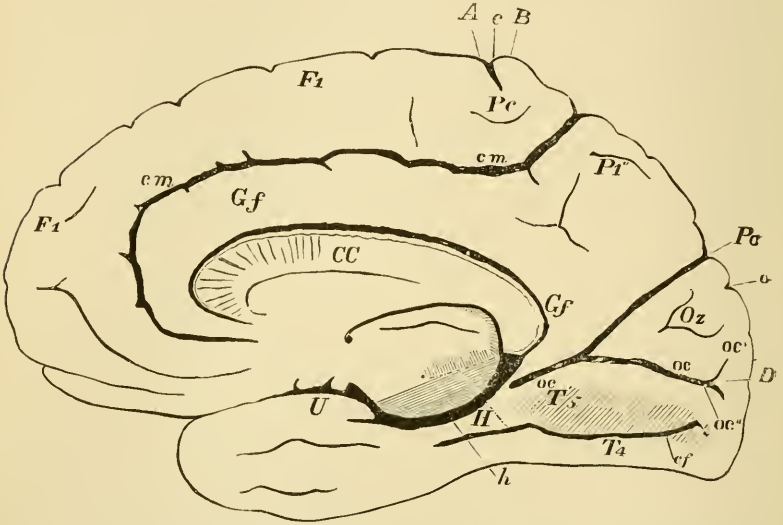


Outer surface of the left hemisphere. The regions bounded by the line (------) represent the territories over which the branches of the anterior cerebral artery are distributed. The regions bounded by the line (— — — — — —) represent the territories over which the branches of the posterior cerebral artery are distributed. *F.* Frontal lobe. *P.* Parietal lobe. *O.* Occipital lobe. *T.* Temporo-sphenoidal lobe. *S.* Fissure of Sylvius. *S'*, Horizontal; *S''*, Ascending ramus of the same. *c.* Sulcus centralis or fissure of Rolando. *A.* Anterior central or ascending frontal convolution. *B.* Posterior central or ascending parietal convolution. F_1, Superior; F_2, Middle, and F_3 Inferior frontal convolution. f_1, Superior, and f_2 Inferior frontal sulcus; f_3 Sulcus præcentralis. P_1, Superior parietal of postero-parietal lobule, viz.: P_2, Gyrus supramarginalis; P'_2, Gyrus angularis. *ip.* Sulcus intraparietalis. *cm.* Termination of the calloso-marginal fissure. O_1 First, O_2 Second, O_3 third occipital convolutions. *po.* Parieto-occipital fissure. *o.* Sulcus occipitalis transversus; o_2, Sulcus occipitalis longitudinalis inferior. T_1, first; T_2, second; T_3, third temporo-sphenoidal convolutions. t_1, first; t_2, second temporo-sphenoidal fissures. (After ECKER and DURET.)

furrow on the under side of the brain, it runs thence outward, backward, and upward, separating the temporal (T, Fig. 374) from the frontal lobe (F), and divides on the outer side of the hemisphere into an anterior (S) and posterior (S') branch, the convolutions included between these two branches, and known as the operculum, covering the insula or island of Reil. An important fissure, readily identified on account of its constant course, is the fissure (c) of Rolando, or central fissure, passing from about the middle line of the hemisphere downward, outward, and forward, reaching very nearly the fissure of Sylvius, and serving to divide the frontal from the parietal lobe. The fissure of Rolando is bordered by two important convolutions running parallel with itself and known as the anterior and posterior central convolutions, or the ascending frontal and ascending parietal convolutions. Through the very constant presence of the long superior frontal (f_1) and inferior frontal fissure (f_2) the latter running into the precentral fissure (f_3), the anterior portion of the frontal lobe naturally divides itself into the superior (F_1), middle (F_2), and inferior (F_3) frontal convolutions. Through the presence of the first and second temporo-sphenoidal fissures in the same manner, the temporal lobe (T) is divided into the first (T_1), second (T_2), and third (T_3) temporo-sphenoidal convolutions. The most important fissure of the parietal lobe (P) is the intraparietal fissure (ip). Starting from the posterior central convolution, it extends backward and downward, and dividing the parietal lobe into the superior (P_1) and inferior (P_2) parietal lobules, terminates toward the posterior extremity of the hemisphere. Beneath the intraparietal fissure, and as constituent parts of the inferior parietal lobule, are situated two important convolutions, the supra-marginal (P_2) convolution arching around the fissure of Sylvius and the angular (P'_2) convolution around the first temporo-sphenoidal fissure. The parietal is separated from the occipital (O) lobe by the parieto-occipital (Po) fissure, the latter being, however, just visible from a lateral view, should be viewed from the mesial surface of the hemisphere, as in Fig. 375, where it (Po) will be observed to descend downward and inward, separating the cuneus (Oz) from the præcuneus (P'_2) and terminating in an acute angle in the calcarine fissure (oc), the latter fissure being so called on account of its marking the inner concave border of the calcar avis or hippocampus minor in the posterior cornu of the lateral ventricle. The occipital lobe (Fig. 374, O) is made up of the first (O_1), second (O_2), and third (O_3) occipital convolutions, the first occipital being separated from the second occipital convolution by the transverse occipital fissure (o), and the second occipital convolution from the third by the inferior longitudinal occipital fissure (o_2). As the calcarine fissure (oc, Fig. 375) does not run into the hippocampal (h) fissure, it will be observed that the convolution lying above the corpus callosum, and known as the gyrus fornicatus (Gf), passes continuously into the convolution of the hippocampus (H). The latter convolution terminates ante-

riorly in a crook-like extremity or crotchet, the so-called uncinate gyrus or subiculum cornu ammonis (U). Below the calcarine fissure are situated two convolutions, the lobulus fusiformis (T_4), and lobulus lingualis (T_5), separated by the occipito-temporal fissure, while above the gyrus fornicatus (Gf) is separated from the mesial surface of the first (F_1) frontal convolution by a well-marked fissure, the calloso-marginal (cm), which, like the parieto-occipital fissure, is also just visible from a lateral view of the hemisphere. It must

FIG. 375.



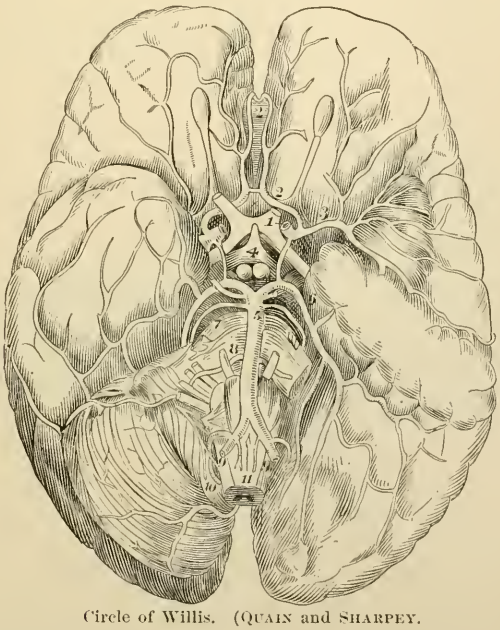
Inner surface of right hemisphere. *CC*. Corpus callosum, longitudinally divided. *Gf*. Gyrus fornicatus. *H*. Gyrus hippocampi. *h*. Sulcus hippocampi. *U*. Uncinate gyrus. *cm*. Sulcus calloso-marginalis. F_1. Median aspect of the first frontal convolution. *c*. Terminal portion of the sulcus centralis, or fissure of Rolando. *A*. Anterior. *B*. Posterior central convolution. P_1''. Præcuneus. *Oz*. Cuneus. *Po*. Parieto-occipital fissure. *o*. Sulcus occipitalis transversus. *oc*, Calcarine fissure; oc'', Inferior ramus of the same. *D*. Gyrus descendens. T_4. Gyrus occipito-temporalis lateralis (lobulus fusiformis). T_5. Gyrus occipito-temporalis medialis (lobulus lingualis). (After ECKER and DURET.)

not be supposed from the fact of names being given to certain well-defined convolutions that the latter are entirely distinct, or do not run into each other; on the contrary, as may be seen from Figs. 374 and 375, it is evident that directly or indirectly they are all continuous with each other. Thus the third frontal (F_3) runs into the anterior (A) central, the latter into the posterior (B) central, the three occipital convolutions into the superior parietal lobule (P), the angular gyrus and third temporo-sphenoidal (T_3) convolutions respectively, and so on. In addition to these principal fissures just mentioned, there are numerous other less important ones which increase considerably the number of convolutions and obscure somewhat those already described. That these fissures are of a secondary character, however, becomes at once evident when the arachnoid and pia mater are removed, they being then seen to be mere superficial indentations and not deep fissures penetrating into the brain.

The internal or white substance of the cerebral hemispheres is

composed largely of fibers which in general radiate from the basal ganglia internally to the gray or cortical substance outwardly. The amount of white substance varies very much in different portions of the hemisphere, thus, in the region of the island of Reil, where the gray substance penetrates to a considerable depth, but little of it is present, whereas, in the posterior portions of the hemisphere, where the gray matter is relatively less well developed, the white substance is present in great quantity. The fibers of which the white substance consists may be said to be essentially of three kinds: First, commissural fibers, such as those composing the corpus callosum or the broad commissure connecting the two hemispheres at the bottom of the great longitudinal fissure or the anterior commissure situated a little in front of the thalami optici and spreading out from the latter into the lower and anterior parts of the temporal lobes. Second, association fibers, or fibers which, lying just beneath the gray matter, connect the different convolutions of the same hemisphere. Third, medullary fibers including both the fibers that connect the cortex cerebri with the basal ganglia, as well as those that pass to and from the cortex through the internal capsule to the crura cerebri and medulla. One of the most striking facts with reference to the cerebral hemispheres, the bulk of the latter being taken into consideration, is the large amount of blood which they receive, one-fifth of the whole mass of the blood probably going to the encephalon

FIG. 376.



Circle of Willis. (QUAIN and SHARPEY.

The manner in which the blood is distributed to the brain is also very remarkable, the branches of the basilar (5) and internal (1) carotid arteries anastomosing so freely, as the circle of Willis (Fig. 376),

that the supply of blood to any one part of the brain is not interrupted, even though the principal branch supplying such a part be obstructed. The importance of this peculiarity in the distribution of the cerebral blood vessels becomes at once apparent when it is remembered that with the cessation of the blood supply the functional activity of the brain at once ceases, and it may be appropriately mentioned in this connection that while in all probability the energy of the brain depends largely on the size of its arteries and the freedom with which the blood circulates through them, the special manifestation of brain power depends upon the particular areas of distribution. It has already been mentioned that the gray matter of the nervous system is more vascular than the white, and that in all probability it is in the gray or vascular substance that the nervous force is generated, the white or fibrous substance transmitting it. The significance, therefore, of the development of the convolutions just described produced through the invaginating of the gray substance into the white, together with their pia mater or vascular tunic, thereby insuring a far greater supply of blood than would be possible if the brain were smooth, becomes evident. Further, when it is borne in mind that the brain is enclosed in a bony, unyielding case, and that the amount of blood sent to the brain from the heart must vary with the force of the latter, and that cerebral disturbances ensue with any increase or diminution in pressure it might be anticipated that some provision must exist by which a uniform pressure within the cerebral substance is maintained. The latter function appears to be fulfilled by the cerebro-spinal fluid found in the subarachnoid cavity of the brain and cord, since if this fluid be withdrawn from a living animal, cerebral disturbances attributable to changes in pressure ensue. The cerebro-spinal fluid amounts to at least two ounces, and probably more, and appears to be as rapidly absorbed as produced, and as it readily passes from the subarachnoid space through the foramen of Magendie or the triangular orifice in the pia mater situated at the inferior angle of the fourth ventricle into the ventricles of the brain or the central canal of the cord, it evidently serves to equalize the pressure in the cranial cavity, merely allowing blood vessels to expand and contract within such limits as do not induce any marked change in the pressure to which the brain substance is usually subjected.[1]

The entire encephalon in the adult male brain weighs on an average about fifty ounces, that of the female a little less, about forty-four ounces. On this supposition, the relative weights of the cerebrum, cerebellum, etc., are as follows:[2]

[1] Magendie, Journal de Physiologie, Tome v., p. 27. Paris, 1825. Tome vii., pp. 1–66, 1827.

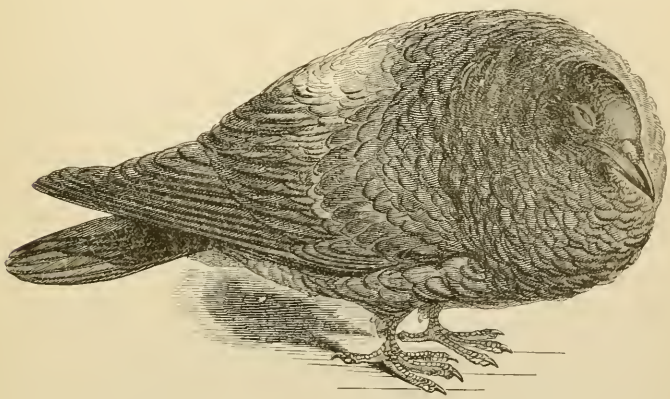
[2] Quain's Anatomy, 8th ed., Vol. ii., p. 581.

Average weight.	Male.		Female.	
Cerebrum	43.98 oz.	1244.63 grammes.	38.75 oz.	1096.62 grammes.
Cerebellum. . . .	5.25 "	148.57 "	4.76 "	134.70 "
Pons and medulla .	0.98 "	27.73 "	1.01 "	28.58 "
Entire encephalon .	50.21 "	1420.93 "	44.52 "	1259.90 "
Ratio of cerebrum to cerebellum.	1 to 8$\frac{4}{5}$		1 to 8$\frac{1}{4}$	

The human brain is absolutely heavier than that of any other animal except the elephant and the cetacea, the brain of the elephant usually weighing from 3622.4 to 4528 grammes[1] (8 to 10 pounds) or even more, that of the young male elephant which died at the Philadelphia Zoölogical Gardens having been found by the author to weigh immediately after removal from the skull 4754.4 grammes (10.5 pounds). The brain of the whale weighs about 2264 grammes (5 pounds);[2] that of a grampus (Delphinus Risso) as found by the author, 3169.6 grammes (7 pounds). Relatively, however, to the size of the body the brain is larger in certain birds and mammals than in man, as, for example, in the canary bird, field mouse, and ouisitite monkey. With reference, however, to the size of the nerves given off from its base, the brain of man is larger than that of any other animal without exception.

In considering the functions of the medulla, pons, cerebellum, and basal ganglia, we have necessarily anticipated somewhat, by a process of exclusion, the functions of the cerebral hemispheres. It only now remains for us to offer the positive evidence bearing upon the questions and confirming the general conclusions already reached by the manner just mentioned.

FIG. 377.



Pigeon, after removal of the hemispheres. (DALTON.)

If the cerebral hemispheres be removed in a pigeon, for example, the animal at once falls into a condition of stupor, its whole appearance being very peculiar and most characteristic (Fig. 377).

[1] Cyclopædia of Anat. Phys., Vol. iii., p. 664. Lond., 1839–47.
[2] Rudolphi, Grundriss der Physiologie, B. ii., s. 12. Berlin, 1823.

With its head almost buried within the feathers of the neck, with closed eyes, the pigeon stands sufficiently firmly, but without moving, apparently utterly indifferent to its surroundings. From time to time it open its eyes, stretches its neck, or smooths its feathers, but soon again relapses to its former condition of apathy. That the pigeon, however, still feels there can be no doubt. Pinch its neck or one of its toes and a persistent effort is made to withdraw the part from the grasp. Fire off a pistol, the pigeon will open its eyes and turn its head round as if it had heard the report and was looking whence it came. The report of the pistol, however, causes no alarm, for the pigeon makes no effort to escape. While the animal undoubtedly hears and sees, the sensations do not give rise to the usual ideas associated with or developed out of them, the pigeon feels but does not perceive the sensation of sound; the report of the pistol does not give rise to any idea of danger usually associated with the production of sound. In the same way the presence of food, though seen and smelt by the pigeon, does not excite the idea of hunger, the animal making no effort to feed, starving to death amidst plenty.[1] That this entire loss of memory, volition and conscious intelligence, following loss of the cerebral hemispheres in a pigeon is not due simply to the effects of shock, hemorrhage, etc., is shown not only by the entirely different effect following destruction of the cerebellum, but that a pigeon from which the cerebral hemispheres have been removed can be kept alive for months by artificial feeding, and, although the effects of shock have long since passed away, nevertheless, the animal never regains its intelligence, remaining ever afterward in this characteristic condition of stupor and apathy. The absence of intelligence that follows the removal of the cerebrum is even more marked in the case of a mammal than in that of the bird. Thus, according to Goltz,[1] a dog in which the cerebrum has been removed is reduced to the condition of a mindless machine, conscious sensations, feelings, emotions, etc., being all wanting. Although the effects of destruction or compression of the cerebral hemispheres in man, whether due to disease or injury, are not as well established as in the case of birds and mammals through the imperfect localization of the disease, the basal ganglia, etc., being usually involved as well as the cerebral hemispheres; nevertheless, a sufficient number of cases have been observed by pathologists which show that loss or compression of the cerebral hemispheres in man involves, as in the case of birds and mammals, the loss of memory, volition, conscious intelligence, the nutritive functions, however, remaining unimpaired. Among such cases may be mentioned that of the sailor related by Sir Astley Cooper,[2] who, having fallen, probably from the yard-arm, was picked up on the deck insensible, practically deprived of all powers of mind, volition, or sensation, in which con-

[1] Pflüger's Archiv, Band xli.

[2] Lectures on the Principles and Practice of Surgery, p. 138. Philadelphia, 1839.

dition he remained for thirteen months, being kept alive all this time by artificial feeding, the grinding of the teeth and the sucking of the lips indicating to his attendants the necessity of giving food and drink. During this period the man lived almost entirely a vegetable existence, the only movements he made, with the exceptions of the lips, etc., being with the fingers, which he moved to-and-fro to the time of the pulse. In this condition the sailor was seen by Cline, the famous surgeon of the day, who, satisfying himself that a depression in the skull existed, trephined, and with the happy result that within a short time after the operation the patient was able to get out of bed, talk, and tell where he came from, his mind having been restored through the removal of the pressure exerted by the depressed bone upon the cerebral hemispheres.

In general, it may be said that injury or disease of the cerebral hemispheres in man entails disturbance or loss of the intellectual powers, according to the seat and extent of the lesion. Impairment and then loss of memory, weakening and failure of the reasoning powers and of the judgment, invariably follow disease or injury of the cerebral hemispheres, while the facts that under such circumstances there is no loss of sensation or motor power, and that the vegetative functions also remain unimpaired, as in the case of idiots and the insane, clearly show that the cerebral hemispheres are indispensable to the manifestation of the intelligence. On the other hand, the fact already mentioned of animals deprived of their cerebral hemispheres living for a longer or shorter time when supplied with food, and of human beings being born anencephalous, and yet were kept alive some time, and who sucked and cried like ordinary infants, proves that the cerebral hemispheres are not concerned in the performance of those functions not involving intellection, which have been assigned to other parts of the encephalon. That the intellectual powers depend upon the development of the encephalon is also shown by the facts of comparative anatomy, the encephalon of the more intelligent animals being much heavier both absolutely and relatively, with reference to the weight of the body, than that of the less intelligent ones. Thus, in fishes the ratio of the encephalon to the body is as 1 to 5,668, in the reptiles as 1 to 1,321, in birds as 1 to 212, in mammals 1 to 189[1] and in man as 1 to 50, supposing the body of the man to weigh 68.1 kil. (150 pounds) and the brain about 1.37 kil. (3 pounds).

Further, the brain of the lowest races of mankind, at least as estimated from their cranial capacity, is not as heavy as that of the higher and more intellectual ones, the brain of the Australian, for example, weighing only 1190 grammes (42 oz.),[2] and correspondingly less bulky. It is also well known that individuals distinguished by

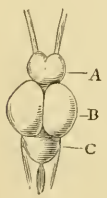
[1] Leuret, Anatomie Comparée du Systeme Nerveux, pp. 153, 234, 284, 422. Paris, 1839.

[2] Davis, Journal of the Acad. of Nat. Sciences, Phila., 1869. Morton, Crania Americana, p. 253, Phila., 1839.

great intellectual power possessed large, heavy brains. Thus the brain of Abercrombie[1] weighed 1783 grammes (63 oz.), that of Cuvier[2] 1820 grammes (64.33 oz.). On the other hand, the brain of idiots has been found in some instances to weigh not more than 566 grammes (20 oz.). It should be mentioned in this connection, however, that the weight of the brain in man depends not only upon race, but on the age, weight, and stature of the individual, and even upon the manner in which the brain is weighed,[3] whether as a whole or in parts, with or without the pia mater and also in reference to the amount of blood it may contain.

It will be observed also from a comparison of the brain of the lower with that of the higher vertebrates, that it is the greater development of the cerebral hemispheres in the latter to which are due the greater bulk and weight of the encephalon. Thus, as we pass from the brain of the fish (Fig. 378) to that of the reptile (Fig. 379), from the brain of the reptile to that of the bird (Fig. 380), from the latter to the brains of mammals (Fig. 381), including that of man, one cannot but be impressed with the fact that the cerebral hemispheres become successively more and more developed

Fig. 378.

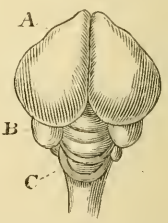


Brain of carp. A. Corpora striata. B. Optic lobes. C. Cerebellum.

Fig. 379.

Brain of lizard.
a. Cerebral hemispheres.
f. Optic lobes.
c. Cerebellum.
e. Medulla.
d. Spinal cord.

Fig. 380.



Brain of the pigeon. A. Cerebral hemispheres. B. Optic lobes. C. Cerebellum.

until in monkeys (Fig. 382) and man they completely cover the cerebellum. Further, it may also be seen from such a comparison that while the brain in fish, reptiles, birds, and the lower orders of mammals, such as the marsupiala, rodentia (Fig. 381), sirenia, etc., is smooth or nearly so, in the higher orders, including the proboscidea, cetacea, the ungulata, the carnivora and primates (Figs. 382, 383), it is more or less convoluted. Indeed, so much is this the case that in the proboscidea it is particularly convoluted, even more so than in man. In general, it may be said that the development of

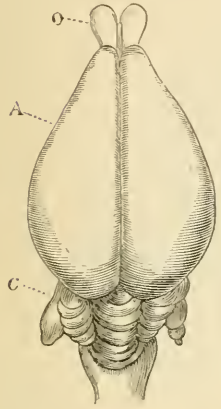
[1] Edinburgh Med. and Surg. Journal, 1845, Vol. lxiii., p. 448.

[2] "Trois livres onze onces quatres gros et demi," is the number given in the account of the autopsy of Cuvier in the Archives générales de Médecine, Tome xxix., p. 144. Paris, 1832.

[3] R. Boyd, Phil. Trans. Lond., Vol. 151, 1862, p. 241.

the intellectual powers depends not only upon that of the encephalon, but more particularly upon that of its cerebral hemispheres, and especially, as affirmed long ago by Erasistratus,[1] upon the

Fig. 381.



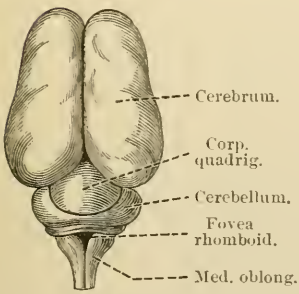
Brain of the rabbit. A. Cerebral hemispheres. O. Olfactory bulb. C. Cerebellum.

Fig. 382.

Brain of the orang.

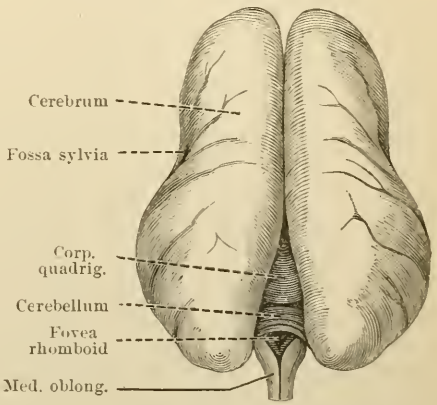
number and depth of the convolutions of the gray matter of the same. Further, in the savage races of mankind, characterized by a low order of intelligence, the convolutions are not so deep, are

Fig. 383.



Brain of human embryo, three months.

Fig. 384.



Brain of human embryo, five months.

less numerous, and are more simply disposed than in the civilized races distinguished by the development of their mental faculties.

[1] Galenus, De Usu Partium, Lib. 8, Cap. 13.

It is well known that in individuals especially remarkable for intellectual power, as in the case of Gauss,[1] for example, a distinguished mathematician, the convolutions of the cerebral hemispheres are found to be very numerous and deep, and far from simply arranged. On the other hand, in idiots the convolutions are few, comparatively superficial, and simply disposed.

The development of the brain also confirms the conclusions based upon the facts of comparative anatomy and ethnology, the transitory stages through which the fœtal brain passes being permanently retained in the brains of the lower animals. Thus, at about three weeks of intrauterine life the brain of the human fœtus resembles that of the adult fish, there being but little difference at this early period in the relative development of the cerebral hemispheres, optic lobes, cerebellum, etc. As development advances the hemispheres enlarge and grow backward; at three months (Fig. 383), though still smooth, they slightly overlap the optic lobes, the latter not having yet divided into the corpora quadrigemina. At about the fifth month (Fig. 384) the cerebral hemispheres in the human fœtus overlap the cerebellum, and here and there exhibit a rudimentary fissure, though their surface is still almost entirely smooth, as in those of the rodentia. Finally, at about the seventh month, the optic lobes are subdivided into the corpora quadrigemina, while at full term or at birth the convolutions are all formed.

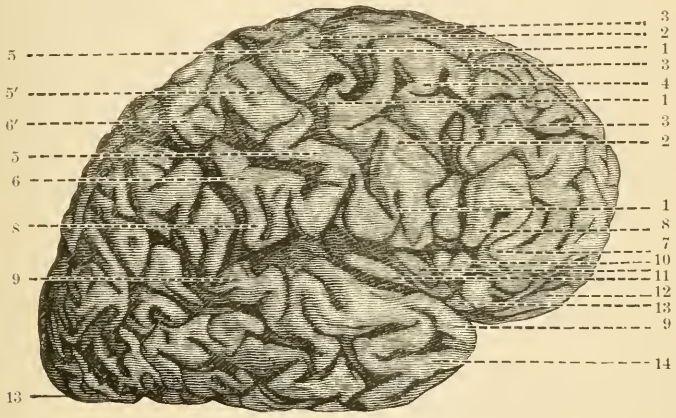
The brain of the human fœtus, however, at this period, both as regards the number, depth, and simplicity of arrangement of the cerebral convolutions, resembles rather the brain of the chimpanzee than that of the adult man, while the brain of the uneducated child resembles, in similar respects, that of the savage races of mankind rather than that of the civilized ones (Fig. 385); a physical correspondence in harmony with their intellectual acquirements. While the facts of experiment, pathology, comparative anatomy, etc., with but few exceptions, and those usually more apparent than real, undoubtedly agree in establishing the view that associates intellectual power with the development of the cerebral hemispheres, and more particularly with that of the convolutions, or the gray matter of the same, it must be borne in mind that the quality of the chemical composition of the latter is quite as important a condition as its mere quantity.

It need hardly be added that the exercise of the mental faculties necessitates the connections between the gray or vesicular substance of the convolutions and the fibers of the white substance being maintained in their normal condition, just as the action of a muscle depends on the position and manner of insertion; and, above all, upon the free supply of blood and active circulation, both that the materials for the nourishment of the hemispheres and the production by them of thought, may be supplied in sufficient quantity, and that the effete and worn-out materials incidental to mental ac-

[1] Quain, Anatomy, 1878, Vol. ii., pp. 529, 581.

tivity may be carried away to the proper emunctories as rapidly as produced. As we have already seen that the different structures of which the encephalon consists, medulla, pons, cerebellum, basal ganglia, cerebral convolutions, etc., have undoubtedly different functions, it is reasonable, therefore, to suppose that the different

FIG. 385.



Cerebrum of man. Lateral view of the right cerebral hemisphere. 1. Fissure of Rolando. 2. Ascending frontal convolution. 3, Superior; 3′, Middle, and 7, Inferior frontal convolutions. 4. A bridging convolution between the superior and middle frontal convolutions. 5. Ascending parietal convolution. 6, 8. Supramarginal convolution (8 in front points to part of the inferior frontal convolution). 9, 9. Superior temporo-sphenoidal convolution. 10, 11, 12. Convolutions of the island of Reil, or central lobe. 13. Orbital convolutions. 14. Lower extremity of middle temporo-sphenoidal convolutions. 15. Occipital lobe. (From SAPPEY after FOVILLE.) ½.

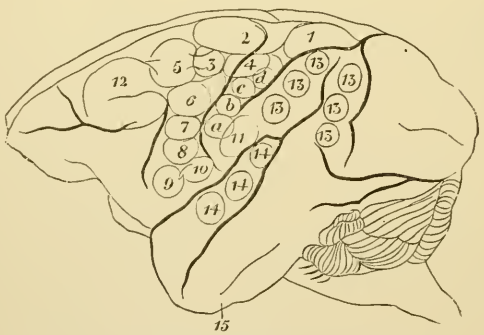
convolutions, or the gray matter of the cerebral hemispheres, have also special faculties or functions. Phrenology has, therefore, a basis worthy of consideration. Phrenology, however, as understood by the vulgar, is based upon the untenable assumption that the form of the surface of the brain can be inferred from the external configuration of the skull, that any protuberance, or "bump," of the latter is to be taken as an indication of a similar excessive development of the former and the possession of some particularly well-developed mental faculty. Apart, however, from the facts that the skull consists of two tables, and that the outer surface of the brain is separated from the inner surface of the skull by the dura mater, arachnoid, pia mater, and cerebro-spinal fluid, the latter variable in quantity, the figure of the brain, except in a general way, does not correspond to the figure of the skull. So much so is this the case that in certain animals, as in the elephant, for example, through the enormous development of the frontal sinuses the anterior portion of the skull is no indication of the form of the brain whatever. Further, the surface of the brain is not elevated into bumps, the convolutions, as we have seen, being formed through the invagination, or dipping down of the gray matter into the white. Even though, then, osseous "bumps" be ever

so well developed, there are never any cerebral "bumps" with special functions or faculties corresponding to the osseous ones. Phrenology, as such, must be relegated, then, to the charlatan and itinerant showman, who amuse their audience by feeling their heads and illustrating their views by showing plaster casts of the heads of Napoleon, Schiller, noted murderers, idiots and the like.

Within recent years, however, another kind of phrenology has been developed and established, more or less satisfactorily based upon entirely different methods of investigation,[1] such as exposing the brain in a living animal, and stimulating with a weak electrical current a particular convolution, and so determining whether the latter is excitable, and whether its stimulation causes sensory or motor effects; or, destroying a particular convolution by cutting, corrosion, etc., and observing whether the animal is deprived of any of its faculties, and so learning whether the convolution has motor or sensory functions.

By such experimental methods it has been established that the convolutions of the brain in animals possesses definite functions, and the same has been shown to be true of the homologous convolutions of the brain in man by experiment, clinical and post-mortem investigation.[2]

FIG. 386.



The left hemisphere of the monkey. (FERRIER.)

Thus, electrical irritation of the convolution bordering the fissure of Rolando in the brain of the monkey (Fig. 386, 1, 2, 3, 4, 5, 6, 7, 8, *a*, *b*, *c*, *d*) and in man[3] (Fig. 387), gives rise to certain well-

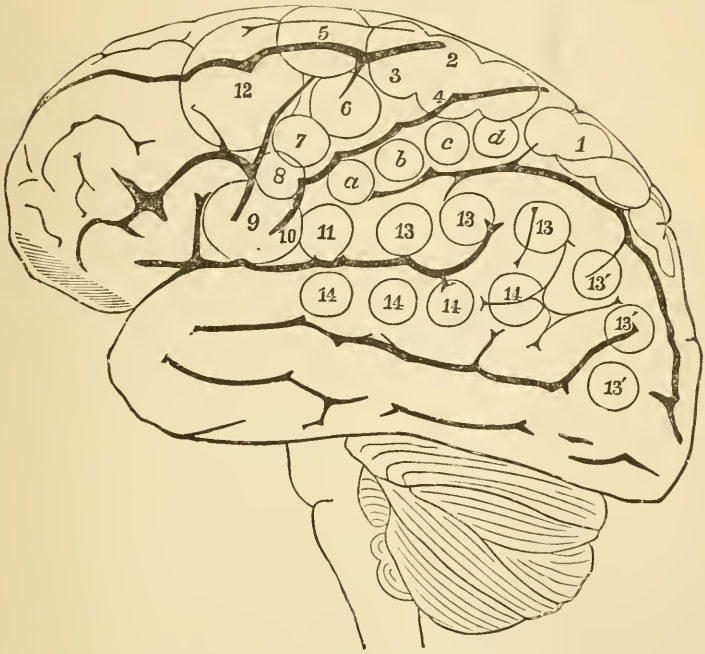
[1] Fritsch and Hitzig, Archiv f. Anat., Physiologie, etc., s. 300, 1870. Ferrier, Functions of the Brain, 1876. Carville and Duret, Archives de Physiologie 2ieme série, Tome ii., p. 352. Paris, 1875. Dalton, New York Medical Journal, 1875, p. 225.

[2] Hughlings Jackson Ferrier, Localization of Cerebral Disease, p. 42. London, 1879. Grasset, Des Localisations dans les Maladies Cérébrales, p. 143. Paris, 1880. Charcot, Leçons sur les Localisations dans les Maladies du Cerveau, p. 166. Paris, 1878. Rendu, Revue des Sciences Médicales, Tome xiii., p. 314. Paris, 1879. Gowers, op. cit., Vol. 2d, p. 15. Mills, op. cit., p. 332.

[3] Bartholow, American Journal of the Medical Sciences, April, 1874.

defined constant movements of the hands, feet, arms, legs, facial muscles, mouth, and tongue, on the opposite side of the body.

FIG. 387.



Lateral view of the human brain. The circles and letters have the same significance as those in the brain of the monkey, Fig. 386. (FERRIER.)

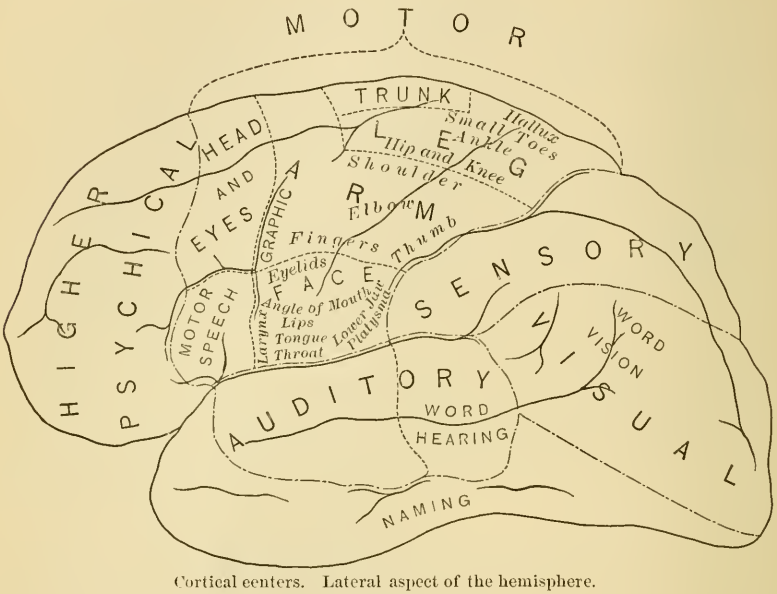
That the muscular contractions induced through electrical stimulation of these or other convolutions are not due to an escape or diffusion downward of the electrical current, and so affecting the corpus striatum, etc., is shown, apart from the fact that stimulation by chemical agents produces the same effect, by several considerations, among which may be mentioned the feebleness of the current used, the close approximation of the electrodes, the imperfect conductivity of the brain substance, the muscular contractions occurring on the opposite side of the body, and not occurring at all when other convolutions were stimulated. That these convolutions are in reality motor centers, constituting the indispensable physical substratum for the volitional, psychical initiation of movements corresponding to those induced by electrical stimulation, the latter acting in the same manner as the stimulus of the will, is further shown by the fact that destruction of these convolutions in the monkey[1] by experiment and in man[2] by disease causes complete hemiplegia of the opposite side of the body without affecting sensation. On the other hand, destruction in the monkey by experi-

[1] Ferrier, Functions of the Brain, 1876, p. 201.

[2] Lepine, De la Localisation dans les Maladies Cérébrales, p. 33. Paris, 1875. Gliky, Deutsches Archiv für klin. Med., Dec., 1875.

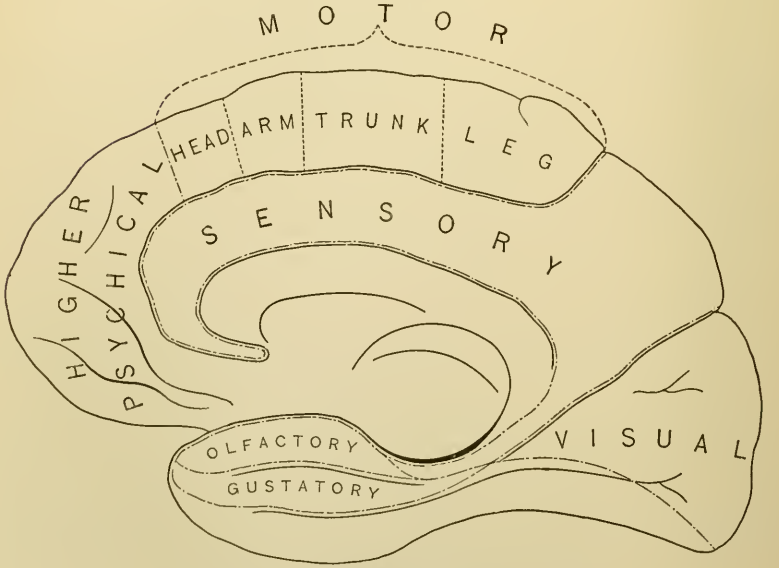
ment[1] and in man[2] by disease of certain convolutions, such as the cuneus, visual area, or temporo-sphenoidal convolutions, auditory area (Figs. 388, 389), while not affecting the motor functions entails

FIG. 388.



Cortical centers. Lateral aspect of the hemisphere.

FIG. 389.



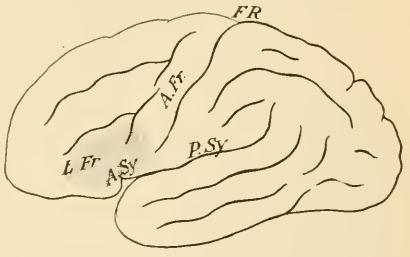
Cortical centers. Mesal aspect of the hemisphere.

[1] Horsley & Schäfer, Phil. Trans., Vol. 179, 1889, p. 1. Beevor & Horsley, Ebend, Vol. 181, 1891, p. 129.

[2] Gowers, op. cit., Vol. 2d, pp. 21, 24.

impairment or entire loss of vision or hearing, according as one or both hemispheres are involved. Such observations prove that there are special sensory as well as motor convolutions in the brain of man. The condition of aphasia, whether presented in the usual, or agraphic, or amnesic form, depending, as, without doubt, it does, upon disease in the region of the posterior extremity of the third left frontal convolution, where the latter abuts on the fissure of Sylvius, and overlaps the island of Reil, is a most convincing argument in favor of the view of the cerebral functions being localized in the convolutions of the hemispheres. Merely referring incidentally to the researches of Petit,[1] Bouillaud,[2] Dax,[3] Broca,[4] Hughlings Jackson,[5] etc., upon the subject of aphasia, the detailed consideration of which belongs rather to the study of clinical medicine and pathological anatomy, it may be briefly said that a person presenting the condition of aphasia as exhibited in its most usual form is deprived of the faculty of articulate speech, though such a person comprehends perfectly the meaning of words spoken by others; having a clear idea of language and of the meaning of words, and being able to write perfectly well. In other cases, however, the patient cannot express ideas in writing (agraphia), or cannot remember the words wanted (amnesia); the idea even of language being lost. That the inability to speak exhibited by the person suffering from aphasia, whether simple or combined with the amnesic or agraphic form, is not due to paralysis of the muscles of articulation is shown by the fact that the aphasic individual makes use of these muscles in mastication and deglutition. Though the center for the coördination of the muscles effecting articulation be diseased, since the action of the center of the articulating muscles is bilateral—that is, the center in one hemisphere innervating the muscles of articulation of both sides—there is no difficulty in understanding that such should be the case.

FIG. 390.



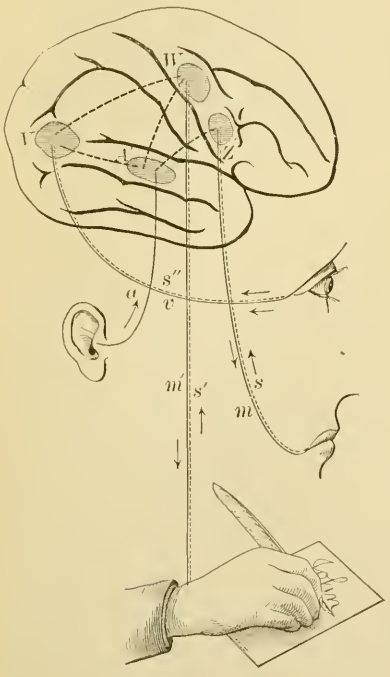
Fr A Sy. Motor speech region in the left hemisphere.

While disease of the center of articulation of the left hemisphere, for the reason just given, does not entail paralysis of the muscles of articulation, it does entail paralysis of articulation or speech, the center for the coördination of the muscles involved in the production of speech being then affected. When it is remembered, however, that speech is gradually acquired through the constant and

[1] Recueil d'obsèrvations d'anatomie et de chirurgie, p. 74. Paris, 1766.
[2] Archives de Médecine, 1825.
[3] Gazette hebdomadaire, April, 1865.
[4] Bulletin de la société anatomique, Tome iv., 1861.
[5] London Hospital Reports, Vol. i.

continual association in the mind of sounds or written signs with the corresponding spoken words, that the acquisition of speech, physiologically speaking, is the development in the brain of an organic nexus between the sound or symbol, and the articulation, it becomes intelligible why if this nexus be broken, that, though the sound be heard and the symbols seen, and the corresponding ideas developed, the words expressing the ideas cannot be uttered, the individual is speechless, because, as Ferrier expresses it,[1] the motor part of the sensori-motor cohesion, sound-articulation situated in the inferior frontal convolution, is broken. Further, owing to the close proximity of the motor center of the hand and facial muscles (Fig. 391), it is easy to see, therefore, why dextral and facial paralysis are so often present, though not necessarily so in the case of aphasia. At first sight it may appear strange that the center for coördinating the muscles effecting articulation should be located exclusively in one hemisphere; in reality, however, there is nothing more strange in this than that most persons are right-handed. Dextral movement, like articulate speech, is gradually acquired, and there is no more reason to doubt that in the absence of the coördinating centers of articulation of the left hemisphere that of the right could be educated, than that in the absence of the right hand one could learn to use the left. Indeed, it has been found that in left-handed persons suffering with aphasia the inferior frontal convolution affected is situated in the right instead of the left hemisphere, as is usually the case. The efferent fibers involved in the production of speech pass from the island of Reil to the knee of the internal capsule, thence through the crusta of the left cerebral peduncle, left half of the pons, to the opposite side of the medulla, from whence emerge the nerves supplying the articulating muscles. It may be mentioned in this connection that in cases of "word blindness," that is where a person, although seeing well in most respects, cannot name a let-

Fig. 391.



Schema to illustrate aphasia. *V*. Visual center. *A*. Auditory center. *W*. Writing center. *Z*. Vocal center. *v* and *a* afferent fibers from larynx and ear. *S S' S''*. Afferent fibers from articulatory, hand and orbital muscles. *m m'*. Efferent fibers from vocal and writing centers. Dotted lines, fibers connecting centers. (Landois.)

[1] Op. cit., p. 274.

ter or word, the cerebral center involved is situated in the angular gyrus (P'_2, Fig. 374), and in cases of "word deafness," where although ordinary sounds are heard words are not, the center is situated in the first temporal convolution (T_1, Fig. 374).[1]

By the same methods made use of in determining the functions of the convolutions about the fissure of Rolando, the angular gyrus, the inferior frontal convolution, etc., the functions of the remaining convolutions have been more or less satisfactorily made out, and may be resumed as follows: (Figs. 387, 388, 389.)

1. Postero-parietal lobule: movement of the hind foot, as in walking.

2, 3, 4. Convolutions bounding the fissure of Rolando: movements of the arm and leg, as in climbing, swimming, etc.

5. Posterior extremity of the superior frontal convolution: extension forward of the arm and hand.

6. Anterior central convolution: supination and flexion of the forearm through action of biceps.

7, 8. Anterior central convolution: elevation and depression of the angle of the mouth, respectively.

9, 10. Inferior or third frontal convolution: movements of the lips and tongue, as in articulation, disease of which causes aphasia.

11. Posterior central convolution: retraction of the angle of the mouth.

a, b, c, d. Posterior central convolution: movements of the hand and wrist, as in clinching the fist.

12. Superior and middle frontal convolutions: lateral movements of the head and eyes, elevation of the eyelids, and dilatation of the pupil.

13. Center of sensation.

13′. Occipital lobe, cuneus, supramarginal lobule, angular gyrus: center of vision.

14. Superior temporo-sphenoidal convolution: center of audition.

V. Subiculum cornu ammonis: centers of olfaction, gustation, etc.

H. Hippocampal region: center of touch.

O. Occipital lobes: centers of organic sensations, hunger.

F. Frontal lobes: intellectual and reflective powers.

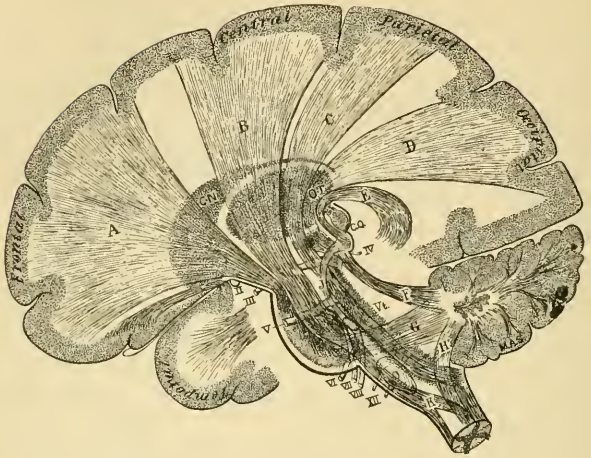
Pituitary Body.

The pituitary body or hypophysis cerebri is not a single organ as the name would imply, but consists of two distinct lobes which differ histologically, in their mode of origin, and functionally. The anterior or glandular lobe is developed as an invagination of the buccal epithelium. It resembles somewhat in its minute structure the thyroid gland, but differs from the latter in being provided with more or less perfect ducts opening between the dura and pia mater.[2] It would appear, therefore, that the "internal secretion" which

[1] Gowers, op. cit., Vol. 2, p. 112.

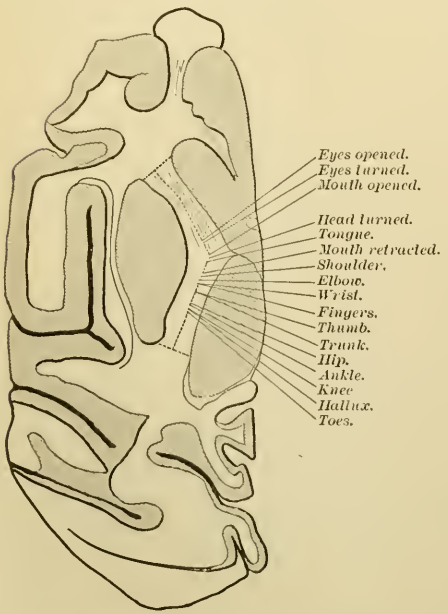
[2] Haller, Morphologisches Jahrbuch, 1896, xxv., s. 31.

FIG. 392.



The projection tracts joining the cortex with lower nerve centers. Sagittal section, showing the arrangements of tracts in the internal capsule. A. Tract from the frontal lobe to the pons, thence to the cerebellar hemisphere of the opposite side. B. Motor tract from the central convolutions to the facial nucleus in the pons and to the spinal cord; its decussation is indicated at K. C. Sensory tract from posterior columns of the cord, through the posterior part of the medulla, pons, crus, and capsule to the parietal lobe. D. Visual tract from the optic thalamus (OT) to the occipital lobe. E. Auditory tract from the intergeniculate body, to which a tract passes from the VIII. N. Nucleus (J) to the temporal lobe. F. Superior cerebellar peduncle. G. Middle cerebellar peduncle. H. Inferior cerebellar peduncle. CN. Caudate nucleus. CQ. Corpora quadrigemina. VT. Fourth ventricle. The numerals refer to the cranial nerves.

FIG. 393.



Schema of the arrangement of the motor fibers in the internal capsula. (BEEVOR and HORSLEY.)

is elaborated fulfills some function in the economy of the brain. The posterior or infundibular lobe is developed as an outgrowth of the brain. Histologically it consists of nerve cells, neuroglia, closed vesicles lined with epithelial cells containing a colloidal material. Less is known even of the functions of the posterior lobe than of the anterior one.

The general course of the tracts connecting the cerebral convolutions whose functions have just been mentioned with the cord are shown in Fig. 392 and the relation of the fibers to each other as they pass through the internal capsule in Fig. 393. The descriptions of

the tracts of the special senses will be deferred, however, until the subjects of olfaction, vision, audition, etc., are considered.

Sleep.

The brain, like every other organ in the body, from time to time must rest, not only that the waste incidental to its functional activity may be repaired, but that its cells or whatever other structural elements concerned in the elaboration of consciousness may not be overtaxed, worn out by constant activity. This need of rest is especially manifest in the case of the brain, for no work is so exhausting as brain work, and when once the brain is fagged, worn out, nothing is so difficult as to restore it to its natural, healthy activity. This necessity of periods of rest rhythmically alternating with those of activity, is undoubtedly the underlying cause of sleep—however the latter may be brought about and concerning which there still prevails considerable difference of opinion among physiologists. Thus it is held by Sommer[1] that as oxygen appears to be gradually stored up during sleep, as shown by the experiments of Pettenkofer, after a time it will have accumulated in such an amount as to accelerate materially the nutritive changes going on in the brain, etc., the effect of which is that awakening occurs. On the other hand, during the waking state this store of oxygen is gradually used up, as shown by increase in the amount of carbon dioxide eliminated, the consequence of which is that exhaustion and general relaxation are experienced, followed by a desire to sleep. According to Pflüger,[2] the combination of this intra-molecular oxygen with the carbon of the brain tissue is so violent as to amount to an explosion, which, taking place at successive intervals, maintains the brain in a waking condition; as the stored-up oxygen, however, is gradually used up the explosions diminish in frequency and violence until they cease altogether, and as a consequence sleep follows. A very plausible theory of the causation of sleep is that advanced by Dr. Cappie,[3] who holds that the molecular activity of the cerebral cells is diminished through less blood being supplied to them by the capillaries, and that consequently the brain occupies less space. But inasmuch as the brain-case must be full, the veins of the pia mater become proportionally distended, the effect of which is that although the absolute quantity of blood, and consequently the pressure remains the same, the direction of the pressure is modified, being less from within and more on the surface of the brain, the latter or the altered direction of the pressure giving rise to sleep. This view is confirmed by the researches of Durham,[4] by whom it was shown that the brain during sleep is in an essentially bloodless condition, that not only the quantity of the blood, but the velocity of its flow is diminished, and also by the

[1] Zeits. f. Rat. Med., Band xxxii., s. 214, 1868. [2] Archiv, 1875, s. 468.
[3] The Causation of Sleep, Edinburgh, 1882.
[4] Guy's Hospital Reports, 3d ser., Vol. vi.

observations of Dr. Hughlings Jackson,[1] who showed by ophthalmoscopic examination that the optic disc during sleep was whiter, the arteries smaller, the veins larger and the adjacent parts of the retina more anæmic than during the waking state.

Among the conditions favoring sleep may be mentioned the cessation of stimuli, diminished excitability of the tissues in response to stimuli, and the quality of the blood. The influence exerted by the latter condition is well shown by the well-known experiment of Mosso,[2] in which the blood of a dog tired out with running was transfused into that of one who had been resting, the effect being that the dog at once showed signs of fatigue and soon went to sleep.

The amount of sleep required is affected by so many conditions, such as age, temperament, habit, mental and physical exhaustion, that it is absurd to lay down any rule upon the subject. In this respect, as in all others physiological, nature is our best guide. The mere fact that some individuals get along with only four or five hours' sleep without their health being affected is no argument whatever that such a small amount of sleep is only required and should suffice for every one. No greater mistake is made, and that so often, by students of medicine, physicians, and literary men generally, than to rob themselves of their natural sleep, at the cost of broken-down health and lost spirits, too often never to be regained. It will be observed that up to the present moment, in our exposition of the functions of the encephalon, we have endeavored to offer only what appears to us to be well-established anatomical and physiological facts, merely mentioning, or not referring at all, to the remaining portions of the encephalon, whose functions have not as yet been made out. It is needless to say, however, that whether or no the different parts of the encephalon and the different convolutions of the hemispheres really possess the functions assigned to them, that the phenomenon of consciousness is thereby in no wise explained. Admitting, for example, that the cuneus is the center of vision, and that the exact nature of the molecular changes occurring in its cells when the perception of sight is experienced were understood, we would be still unable to understand how the vibrations of light falling upon the retina give rise ultimately to visual perceptions—that is, the manner in which a physical impression becomes a conscious perception. In the present state, at least, of the development of our consciousness it appears impossible even to conceive of how the gap between matter and mind, the objective and subjective, can ever be bridged over. We can say that the brain is the organ of the mind, even that it converts heat into thought, but, as viewed subjectively, the functions of the brain are synonymous with mental operations. The phenomenon of consciousness must be studied, not only objectively by the physiologist, but subjectively by the psychologist; nevertheless, too much stress must not be laid upon

[1] Royal London Ophth. Hosp. Reports.
[2] Du Bois Reymond, Archiv, 1890, s. 89.

the distinction of matter and mind, of object and subject, as made by the metaphysician, since the existence of matter or mind, as shown by ultimate analysis, is only an inference. We are conscious of the perceptions of hardness, roundness, weight, extension, etc., and we infer the existence of something underlying these qualities, which we call matter, and which produces in us these sensations. We are directly conscious of these perceptions, not of the matter supposed to cause them. The existence of matter being, therefore, an inference from our consciousness, it is impossible to say, not knowing anything whatever about its nature, whether it is akin to mind or not. On the other hand, suppose that matter does exist, it is certain that the various modes of motion ordinarily known as heat, light, sound, etc., are transformable in us into equivalent modes of consciousness, and we infer from these modes of motion the existence of something, the mind underlying these modes of consciousness, but of whose nature we know just as little as that of the matter, from the effects of which its existence is inferred. The idealist may argue that there is no such thing as matter apart from mind, since material forces are only cognizable as modes of consciousness, and the materialist may argue that there is no mind apart from matter, that the modes of consciousness are material, since what exists in us as consciousness is transformable into modes of motion, but it is evident that the forces of the inner are correlated with those of the outer world, the forces of the outer with those of the inner world, that if we begin with mind we end with matter, if with matter we end in mind; matter and mind being merely symbols of the unknown reality underlying both.[1]

[1] Herbert Spencer, First Principles, p. 558.

CHAPTER XXXV.

THE NERVOUS SYSTEM.—(*Continued.*)

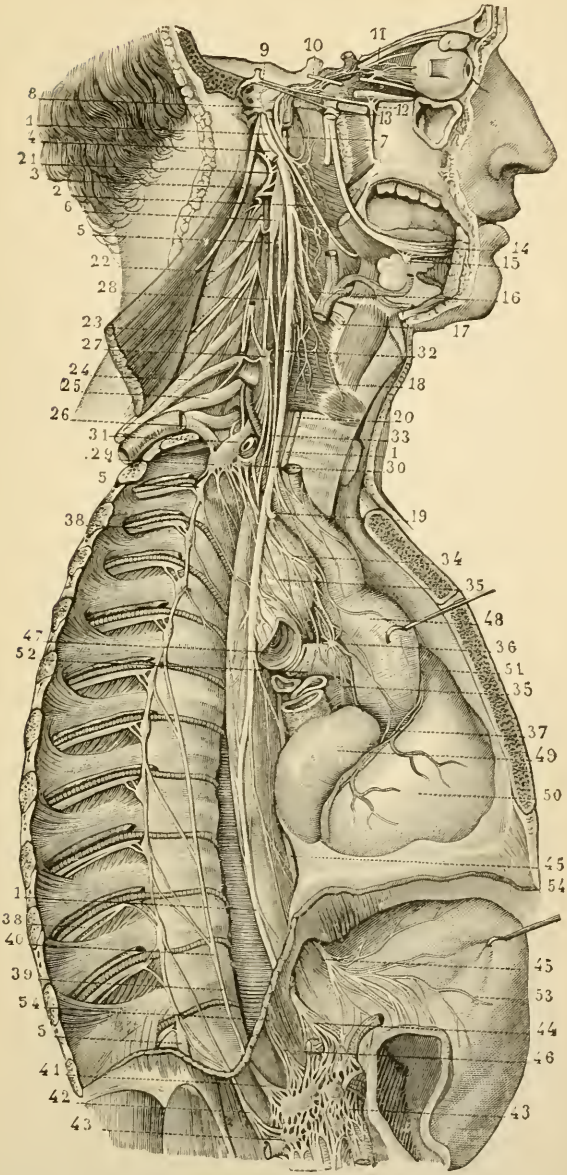
SYMPATHETIC NERVOUS SYSTEM.

The sympathetic system of nerves, or the system of organic vegetative life, also known as the trisplanchnic nerve, great intercostal nerve, etc., consists of a double chain of symmetrically disposed ganglia extending the entire length of the vertebral column, which, gradually converging, terminates finally as a single ganglion, the ganglion impar, resting upon the coccyx. While there is no doubt as to the manner in which the double ganglionated cord of which the sympathetic consists ends, it has not as yet been made out exactly how it begins; the observation of Ribes[1] that it begins as it ends, in a ganglion impar situated upon the anterior communicating artery, not having been confirmed by other anatomists. Intercommunicating with the nerves of the cerebro-spinal system, and giving off during its course numerous branches forming intricate plexuses, such as the cardiac, solar, and hypogastric, the sympathetic nerves, as a general rule, follow the course of the great blood vessels, entwining the latter as the ivy the oak, to supply the viscera of the great cavities of the body, etc.

The nerves of the sympathetic system are usually much smaller, softer, and less distinctly seen than those of the cerebro-spinal system, present a grayish aspect, and adhere closely, by connective tissue, to contiguous structures. While consisting of medullated nerve fibers, they are largely composed of the pale gray, gelatinous fibers of Remak, the latter resembling embryonic nerve fibers and the nerve fibers developed in the reunion of nerves. The ganglia of the sympathetic, whether of the ganglionated cord or its branches, do not differ essentially in structure from the ganglia of the posterior roots of the spinal nerves, large root of the fifth, trigeminal, glosso-pharyngeal, pneumogastric, etc. They consist of a mass of nerve cells smaller than those of the spinal ganglia, imbedded in a stroma of connective tissue, which is traversed by nerve fibers, the whole being enclosed by a tightly adherent membrane continuous with the sheath of the nerves upon which the ganglia occur, the latter looking like so many grayish-white or reddish-gray swellings or knots. The main ganglia and branches of the sympathetic being situated in the cervical, thoracic, abdominal, and pelvic regions, we may begin in our necessarily brief account of the physiological relation of the parts involved with the ganglia of the cervical region, and first with the superior cervical ganglion (Fig. 394).

[1] Mem. de la Soc. Med. d'Emulation, Tome viii., p. 606.

FIG. 394.



Cervical and thoracic portion of the sympathetic. 1, 1, 1. Right pneumogastric. 2. Glossopharyngeal. 3. Spinal accessory. 4. Divided trunk of the sublingual. 5, 5, 5. Chain of ganglia of the sympathetic. 6. Superior cervical ganglion. 7. Branches from this ganglion to the carotid. 8. Nerve of Jacobson. 9. Two filaments from the facial, one to the spheno-palatine and the other to the otic ganglion. 10. Motor oculi externus. 11. Ophthalmic ganglion, receiving a motor filament from the motor oculi communis and a sensory filament from the nasal branch of the fifth. 12. Spheno-palatine ganglion. 13. Otic ganglion. 14. Lingual branch of the fifth nerve. 15. Submaxillary ganglion. 16, 17. Superior laryngeal nerve. 18. External laryngeal nerve. 19, 20. Recurrent laryngeal nerve. 21, 22, 23. Anterior branches of the upper four cervical nerves, sending filaments to the superior cervical sympathetic ganglion. 24. Anterior branches of the fifth and sixth cervical nerves, sending filaments to the middle cervical ganglion. 25, 26. Anterior

branches of the seventh and eighth cervical and the first dorsal nerves, sending filaments to the inferior cervical ganglion. 27. Middle cervical ganglion. 28. Cord connecting the two ganglia. 29. Inferior cervical ganglion. 30, 31. Filaments connecting this with the middle ganglion. 32. Superior cardiac nerve. 33. Middle cardiac nerve. 34. Inferior cardiac nerve. 35, 35. Cardiac plexus. 36. Ganglion of the cardiac plexus. 37. Nerve following the right coronary artery. 38, 38. Intercostal nerves, with their two filaments of communication with the thoracic ganglia. 39, 40, 41. Great splanchnic nerve. 42. Lesser splanchnic nerve. 43, 43. Solar plexus. 44. Left pneumogastric. 45. Right pneumogastric. 46. Lower end of the phrenic nerve. 47. Section of the right bronchus. 48. Arch of the aorta. 49. Right auricle. 50. Right ventricle. 51, 52. Pulmonary artery. 53. Right half of the stomach. 54. Section of the diaphragm. (SAPPEY.)

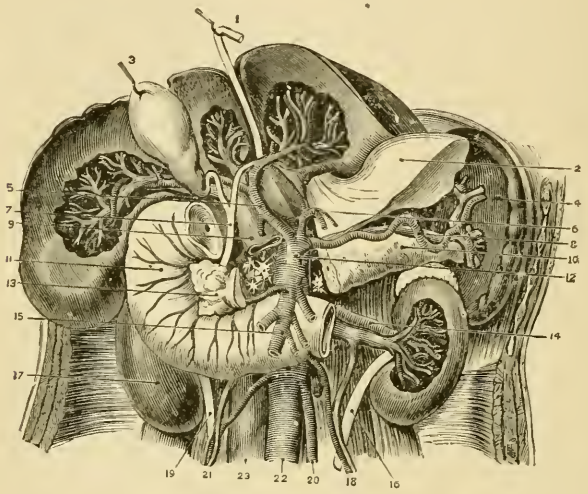
The superior or first cervical ganglion, lying upon the rectus major muscle opposite the second and third cervical vertebræ and behind the internal carotid artery, is connected by intervening filaments with the upper four spinal nerves—the ganglia of the glosso-pharyngeal, pneumogastric, and the hypo-glossal nerves. In addition to its cord of communication with the second cervical ganglion, the superior cervical gives off an ascending branch, vascular and pharyngeal branches, and the superior cardiac nerve. The ascending branch accompanying the internal carotid artery through the carotid canal divides into two branches, which, subdividing and communicating with each other around the artery, so form the carotid plexus. From the latter are given off filaments to the abducens nerve, and the deep petrosal which passes to the spheno-palatine, or Meckel's ganglion, the latter connected with the spinal system by the superior maxillary and great petrosal nerve. Continuing upward around the artery, on reaching the cavernous sinus, the sympathetic plexus becomes then the cavernous plexus, an important one, since it communicates with the semilunar ganglion and ophthalmic branch of the trigeminal with the ophthalmic ganglion, the latter connected with the spinal system by the ophthalmic and oculo-motor nerves, and with the oculo-motor and pathetic nerves. From the carotid and cavernous plexuses fine filaments are also given off which entwine themselves around all the branches of the internal carotid artery. The vascular branches of the superior cervical ganglion form plexuses upon the internal carotid artery and its branches. By the plexuses on the internal, maxillary, and facial arteries the sympathetic communicates with the otic and submaxillary ganglia respectively, the otic ganglion being connected with the spinal system by the small petrosal, the submaxillary ganglia by the chorda tympani. The pharyngeal branches, two or three in number, descending to the side of the pharynx, together with branches from the glosso-pharyngeal and pneumogastric nerves, form the pharyngeal plexus, which, as we have already mentioned, supplies the mucous membrane and constrictor muscles of the pharynx. The superior cardiac nerve, derived from the first cervical ganglion and from the cord below it, descends behind the great blood vessels of the neck, and entering the thorax passes on the right side either in front of or behind the subclavian artery, thence along the innominate to the back of the arch of the aorta, to end in the cardiac plexus. On the left side the nerve follows the carotid artery in its course to the cardiac plexus.

The superior cardiac nerve communicates with the pneumogastric, and gives off filaments to the inferior thyroid artery. The middle, or second cervical ganglion, resting upon the inferior thyroid artery, and situated opposite the fifth cervical vertebra, is connected with the third cervical ganglion by several branches, and gives off filaments to the fifth and sixth spinal nerves, branches which follow the inferior thyroid artery to the thyroid body, and the middle cardiac nerve. The latter, as it descends the neck, receives filaments from the superior and inferior cardiac and pneumogastric nerve, and ends in the cardiac plexus. Occasionally the middle cervical ganglion is indistinct, or even absent; in such cases it appears to be fused with the inferior or third cervical ganglion. The latter, situated behind the vertebral artery and between the transverse process of the last cervical vertebra and the first rib, gives off, in addition to the branches going to the first thoracic ganglion, branches to the seventh and eighth spinal nerves, to the vertebral artery, and the inferior cardiac nerve, which, after receiving filaments from the middle cardiac and inferior laryngeal nerves, and sometimes from the first thoracic ganglion, terminates in the cardiac plexus. Occasionally the inferior cardiac nerve of the left side becomes blended with the middle cardiac nerve. The three cardiac and pneumogastric nerves, together with branches from the first thoracic ganglion, form the cardiac plexus. The latter situated behind and beneath the arch of the aorta, gives off branches which, accompanying the coronary arteries, constitute the coronary plexuses.

While the cervical portion of the sympathetic consists, as we have seen, of three ganglia, etc., the thoracic portion consists of usually twelve ganglia, resting upon the heads of the ribs and covered by the pleura. The first thoracic ganglion, as already mentioned, is connected with the last cervical, and the last thoracic with the first lumbar, the connecting cord of the latter passing through the diaphragm. Each thoracic ganglion usually gives off two narrow cords, the rami communicantes, which pass to the nearest intercostal nerve. The upper six thoracic ganglia give off, also, branches to the aorta, intercostal blood vessels, and the œsophageal and pulmonary plexuses of the pneumogastric nerve. The lower six thoracic ganglia give off, in addition to the branches going to the aorta, branches which go to form the three splanchnic nerves. The great splanchnic nerve, deriving its roots from the sixth to the tenth thoracic ganglia, inclusive, perforates the crus of the diaphragm, and terminates in the semilunar ganglion. The small splanchnic nerve, deriving its roots from the tenth and eleventh thoracic ganglia, passes through the diaphragm with the preceding nerve, and terminates in the solar plexus. The third splanchnic, sometimes absent, coming from the twelfth thoracic ganglion, pierces the diaphragm, and terminates in the renal plexus.

The solar plexus (Fig. 395), so called on account of the numerous filaments radiating from it, is situated behind the stomach and in front of the aorta and crura of the diaphragm, and surrounding the cœliac and commencement of the superior mesenteric artery, extends to between the suprarenal bodies. It consists of an intricate mixture of nerves and ganglia; among the former may be men-

FIG. 395.



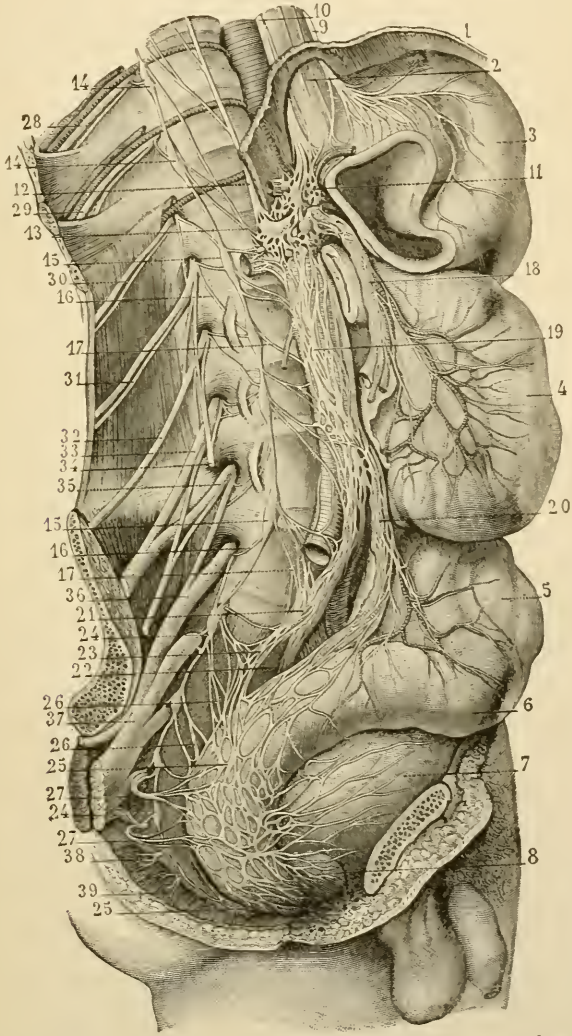
Solar plexus. (HIRSCHFELD.)

tioned the great and small splanchnics, as well as filaments from the pneumogastric nerve; among the latter the semilunar ganglion (Fig. 396), so called on account of its being situated on each side of the plexus, at the side of the cœliac and superior mesenteric arteries. From the solar plexus emanate numerous plexuses, named after the vessels around which the branches entwine themselves, as follows: the phrenic, coronary, hepatic, splenic, suprarenal, renal, and spermatic, superior mesenteric, and aortic plexus. The aortic plexus, descending upon the aorta from the solar plexus, of which it is the continuation, after giving off the inferior mesenteric plexus terminates below in the hypogastric plexus. The latter very intricate plexus, situated between the common iliac blood vessels, extends downward as the inferior hypogastric plexus on each side of the rectum, and after receiving branches from the lower lumbar and sacral ganglia, the lower two or three sacral nerves, and the inferior mesenteric plexus, gives off the vesico-prostatic, or the vesico-vaginal and uterine plexuses, according to the sex respectively.

The lumbar portion of the sympathetic (Fig. 396) consists of four or five ganglia situated at the sides of the vertebræ which communicate with each other, and with the adjacent lumbar nerves, as in the case of the thoracic ganglia, and give off branches to the aortic and

hypogastric plexus. The sacral ganglia, usually four in number, are connected likewise with the spinal nerves, and give off branches to the hypogastric plexus. As already mentioned, the single coccygeal ganglion or ganglion impar, with connections similar to those of the sacral ganglia, is common to the two sympathetic nerves. While

FIG. 336.



Lumbar and sacral portions of the sympathetic. 1. Section of the diaphragm. 2. Lower end of the œsophagus. 3. Left half of the stomach. 4. Small intestine. 5. Sigmoid flexure of the colon. 6. Rectum. 7. Bladder. 8. Prostate. 9. Lower end of the left pneumogastric. 10. Lower end of the right pneumogastric. 11. Solar plexus. 12. Lower end of the great splanchnic nerve. 13. Lower end of the lesser splanchnic nerve. 14, 14. Last two thoracic ganglia. 15, 15. The four lumbar ganglia. 16, 16, 17, 17. Branches from the lumbar ganglia. 18. Superior mesenteric plexus. 19, 21, 22, 23. Aortic lumbar plexus. 20. Inferior mesenteric plexus. 24, 24. Sacral portion of the sympathetic. 25, 25, 26, 26, 27, 27. Hypogastric plexus. 28, 29, 30. Tenth, eleventh, and twelfth dorsal nerves. 31, 32, 33, 34, 35, 36, 37, 38, 39. Lumbar and sacral nerves. (SAPPEY.)

considerable difference of opinion prevailed at one time as to whether the ganglia of the sympathetic were sensitive, there is no doubt on this point at present; mechanical or chemical irritation of the thoracic or semilunar ganglia in dogs, calves, and rabbits, having been shown by Flourens,[1] Brachet,[2] Muller,[3] Longet,[4] etc., to give rise to pain. The sensibility of the sympathetic, however, is far from acute, being indeed, dull, as compared with that of the cerebro-spinal system. As regards the excitability of the sympathetic, it has also been shown by Muller,[5] Longet,[6] and others, that stimulation of the ganglia, splanchnic nerves, etc., by electricity or chemical irritants causes contractions of the muscular coat of the intestines. Inasmuch, however, as the muscular coat of the intestines consists of unstriated muscular tissue, the contraction does not immediately follow the stimulation, as in the case of the cerebro-spinal system and striated muscle, and further, the contraction lasts longer, another characteristic of the effect of stimulating unstriated muscular tissue. Since, however, the most important effects following stimulation of the sympathetic can be obtained, as we shall see presently, by the stimulating of the cerebro-spinal system, and as the ganglia and fibers of the sympathetic lose their properties through atrophy, degeneration, etc., when separated from the cerebro-spinal system, with which we have just seen they are invariably connected, as shown by the experiments of Bernard,[7] Courvoisier,[8] etc., it would appear that whatever properties are possessed by the sympathetic are due to its connections with the cerebro-spinal system. That the sympathetic system, in fact, is only an appendage of the cerebro-spinal system, is not only shown by the facts just referred to, but also by the very important one in this connection that in the lowest fishes, amphioxus, myxine, the sympathetic system is undeveloped or absent, which would not be the case were its presence an indispensable element in the nervous organization of a vertebrate. Up to the beginning of the eighteenth century it may be said that absolutely nothing had been definitely established with regard to the functions of the sympathetic system. In 1712, however, Pourfour du Petit[9] divided the cervical sympathetic in a dog, repeating the experiment in 1725, in the presence of Winslow and Senac, and called attention among its consequences to the redness and injected condition of the conjunctiva, the contracted condition of the pupil,[10] etc. The conclusion drawn by

[1] Recherches expérimentale sur les propriétés et les functions du systeme nerveux, p. 230. Paris, 1842.

[2] Recherches experimentale sur les functions du système ganglionaire, p. 305. Bruxelles, 1834. [3] Muller, Physiology, Vol. i., p. 712. London, 1840.

[4] Physiologie, Tome iii., p. 593. Paris, 1869. [5] Op. cit., p. 713.

[6] Op. cit., p. 595, Systeme Nerveux, Tome ii., p. 568. Paris, 1842.

[7] Journal de la physiologie, Tome v., p. 407. Paris, 1862.

[8] Archiv of Micros. Anat., Band ii., s. 30. Bonn, 1886.

[9] Memoires de l'Acad. des Sciences, p. 1. Paris, 1827.

[10] Due to the unopposed action of the third pair of nerves supplying the circular muscular fibers of the iris.

Petit from his experiments and observations was that the intercostal nerve, as the sympathetic was then called, "furnished spirits to the conjunctiva, to the glands, and to the vessels which are found in these parts, the relaxation of the parts being so evident that there almost always ensues a slight inflammation of the conjunctiva due to the swelling of the vessels;" that the influence exerted by the sympathetic was propagated from below upward toward the brain, and not from the brain downward, as was often supposed. Notwithstanding the importance of the conclusions correctly drawn from his experiments by Petit with reference to the influence of the sympathetic upon the circulation, nutrition of the eye, etc., nearly a century passed without anything further being added to our knowledge of the functions of the sympathetic. In 1812, however, Dupuy, of Alfort, having removed the superior cervical ganglion in horses, called attention among the effects of the experiment, particularly to the injected condition of the ocular conjunctiva, and to the elevation of temperature in the ears, head, and neck, which were bathed in sweat; the general conclusion arrived at by Dupuy[1] being that the sympathetic exercises a great influence on the nutritive functions. While Petit described the effects of cutting the cervical sympathetic, and Dupuy of removing the superior cervical ganglion, neither of these experimenters offered any definite explanation of the hyperæmia noted in both cases, nor Dupuy of the rise in temperature in the latter one. Indeed, the true explanation of the phenomena at that period would have been impossible, the structure of the arteries not yet being understood.

Even though Valentin[2] had shown, in 1839, that the arteries contracted in response to stimulation of the nerves distributed to them, it was not admitted that the middle coat of the arteries contained muscular fibers until 1840, when such was actually demonstrated to be the case beyond doubt by Henle.[3] During the same year, Stilling,[4] like Henle, was led to the conclusion that there existed nerves comparable to those distributed to the muscles generally, which act upon the blood vessels, either directly or reflexly, and which he called "vasomotor nerves." In 1852 Brown-Séquard[5] divided the cervical sympathetic on one side in rabbits, and called attention, as Bernard[6] had done in the previous year, to the hyperæmia and elevation of temperature, often amounting to as much as 11° F. (6.1° Cent.) on the corresponding side of the head and ear, and for the first time gave the true explanation of the phenomena in attributing the rise in temperature of the parts affected

[1] Journal de Corvisart et Leroux, 1816, Tome xxxvii., p. 340. Meckel's Archiv, 1818, Band iv., s. 105.

[2] De Functionibus Nervorum Cerebralium et Nervi Sympathetici, p. 153. Bernæ, 1839.

[3] Wochenschrift für die gesammte Heilkunde, 1840, No. 29, s. 329.

[4] Recherches path. et med. pratiques sur l'irritation. Leipzig, 1840.

[5] The Medical Examiner, New Series, Vol. viii., p. 489. Philadelphia, August, 1852.

[6] Comptes rendus de la société de biologie, Tome iii., p. 163. Paris, 1851.

to the supply of blood being increased through the dilatation of the blood vessels, and by showing that while section of the sympathetic in paralyzing the muscular coats of the arteries permits of their dilatation, electrical stimulation of the central cut end of the sympathetic causes their contraction again, and with the latter the restoration of the parts to their normal condition. To Brown-Séquard must be accorded, therefore, the discovery, not exactly of vasomotor nerves, since the existence of such had been previously indicated by Henle and Stilling, but, more especially, of the vaso-constrictor nerves of the cervical sympathetic, and of their mode of action in influencing the calibre of the blood vessels, temperature, etc., of the parts to which the latter are distributed. It should be mentioned, however, in justice to Bernard, that three months after Brown-Séquard's discovery, and without being aware of it, Bernard[1] offered the same explanation of the experiments performed by him during the previous year (1851), but at that time by him incorrectly interpreted.

The calibre of the veins as well as that of the arteries is regulated by vaso-constrictor nerves. Thus, for example, stimulation of the peripheral cut end of the splanchnic nerve causes contraction of the portal vein[2] and of the sciatic nerve, the femoral artery being ligated, contraction of the superficial veins of the limb.[3] The modification in calibre of blood vessels due to the action of vaso-constrictor nerves can be shown not only by the methods just mentioned, but also by measuring the amount of blood that flows from a vein before and after stimulation of the vaso-constrictor nerve supplying it, the outflow being much less in the latter than in the former case. Another method also made use of is based upon the fact that stimulation of a vaso-constrictor nerve in contracting the blood vessels of a limb will cause a rise of blood pressure in that limb, the general blood pressure remaining however unaltered, as shown by means of a manometer connected with the opposite limb.

Contractions of the blood vessels in a limb as due to vasomotor influence can also be studied by means of the plethysmograph of Mosso, already described, the contractions of the vessels being shown by the diminution in the volume of the limb used, the latter being indicated by the fall of the recording lever.

The vaso-constrictor nerves are found not only in the cervical, but also in the thoracic and abdominal portions of the sympathetic, and in the trachial and sciatic plexuses, supplying the upper and lower extremities. While the vaso-constrictor nerves are given off as fibers from the cells of the sympathetic ganglia, the latter are in relation functionally with the axons that pass from the cells situated in the cord at different levels, they being in turn in relation with the axons that descend from cells in the medulla. Hence, division

[1] Ibid., 1852, Tome iv., p. 169.
[2] Mall, Du Bois Reymond Archiv, 1890, s. 57 ; 1892, s. 409.
[3] Thompson, Du Bois Reymond Archiv, 1893, s. 104.

or stimulation of the peripheral cut ends of the medulla cord, or of certain spinal nerves in certain definite regions, is followed by dilatations or contractions of the blood vessels, just as if the vaso-constrictor nerves had themselves been divided or stimulated.[1] Thus, for example, while the vaso-constrictor nerves of the head are derived from the superior cervical ganglion, they can be traced indirectly by their division and electrical stimulation through the cervical cord of the sympathetic to the anterior roots of the first three dorsal spinal nerves, and thence into the anterior columns of the cord. Further, according to Bernard,[2] whilst the fibers distributed to the dilating muscular fibers of the iris, thereby causing dilation of the pupil, are derived from the first two dorsal nerves (cilio-spinal center), those distributed and influencing the caliber of the blood vessels are derived from the third dorsal nerve. In the same manner, the vaso-constrictor nerves supplying the blood vessels of the upper extremity, while emanating from the first thoracic ganglion, are, functionally, derived from the spinal cord, passing off from the latter with the anterior roots of the third to the seventh dorsal nerves inclusive, and thence traversing the thoracic portion of the sympathetic and the inferior thoracic ganglion, reach the brachial plexus by the rami communicantes, to be finally distributed with the branches of the plexus, while such of the vaso-constrictor nerves as are derived from the plexus itself are given off with the anterior roots of the cervical nerves. The vaso-constrictor nerves supplying the blood vessels of the abdominal viscera, more especially the splanchnic nerves, are largely derived from the dorsal and lumbar portion of the cord; the latter, together with the sacral portion of the cord, giving off fibers which pass through the lumbar and sacral plexuses to the sympathetic, and thence into the lower extremities, supplying the blood vessels of the latter.

Inasmuch, then, as the vaso-constrictor nerves are derived from the spinal cord, traversing more particularly its anterior columns, it might naturally be supposed that all these nerve fibers at some point of the cord, the upper portion most probably, would be brought to a focus, so to speak, and that stimulation of such a portion of the cord would cause all of the blood vessels to contract and a corresponding rise in blood pressure and division of the same, a dilatation of the vessels and fall in blood pressure.

Such a focus or vasomotor center has indeed been found in animals, not exactly by anatomical demonstration, but by means of successive sections of the cord below upward, and from above downward, and localized in the rabbit, for example, by Owsjanikow[3] and Dittmar[4] in the floor of the fourth ventricle on either side of the middle line just one millimeter behind the optic lobes and

[1] Budge and Waller, Comptes rendus, Tome xxxiii., p. 372. Paris, 1851. Ludwig and Thiry, Wiener Sitzungsberichte, 1864, Band xlix. II. Abtheilung, s. 421. Vulpian, Leçons sur l'Appareil vaso moteur, p. 189. Paris, 1875.

[2] Comptes rendus, Tome iv., p. 383.

[3] Ludwig's Arbeiten, 1871, s. 210.

[4] Ebenda, 1873, s. 110.

extending about four millimeters towards the net of the calamus scriptorius.

From this "tonic" center emanate impulses, which transmitted through the anterior columns of the cord and anterior roots of the spinal nerves pass thence to the sympathetic ganglia and vaso-constrictor nerves, and through the latter maintain the normal calibre of the vessels or the vascular tonus.

It has also been established[1] that vaso-constrictor centers exist in the spinal cord, since after section of the cord the tonicity of the vessels below the seat of section is to a certain extent still maintained. That the sympathetic ganglia contain also vaso-constrictor centers is shown by the fact of the tonicity of the vessels in the limb of a dog being maintained even after removal of a considerable portion of the spinal cord.[2] The action of the centers in the cord and sympathetic ganglia is usually regarded, however, as being of a secondary character to that excited by the principal center in the medulla.

Inasmuch as the muscular fibers of the middle coat of the blood vessels are disposed in a circular manner at right angles to the long axis of the vessels, it is not difficult to understand why stimulation of the vaso-constrictor nerves is followed by contraction of the vessels—indeed, the disposition of the nervous and muscular fibers being such, it can hardly be conceived how it should be otherwise, and yet, strange as it may appear, as first shown by Bernard,[3] there are also nerves the stimulation of which causes dilatation of the blood vessels instead of contraction, and which may, therefore, be called vaso-dilator nerves; among such may be mentioned the chorda-tympani, the auriculo-temporal, the nervi-erigentes of the penis; stimulation of these nerves causing dilatation of the vessels of the tongue,[4] of the ear, and of the corpora cavernosa of the penis,[5] respectively. Though numerous explanations have been offered of the manner in which the vaso-dilator nerves act, it must be admitted that none of them are satisfactory, and that it is not yet understood how their stimulation causes dilatation of the blood vessels. Thus, it has been said that the stimulation of a vaso-dilator nerve causes the vein of the part to contract, and that in consequence an obstacle is offered to the passage of the blood from the artery to the capillary, which is the cause of the dilatation of the artery. As a matter of fact, however, the vein does not contract, but dilates as much as the artery. It has also been suggested that the stimulation of a vaso-dilator nerve excites the activity of the anatomical elements of the part to which the nerve is distributed, the effect of which in the case of a salivary gland, for example, would be that

[1] Goltz u. Freusberg, Pflüger's Archiv, 1874, s. 463.

[2] Goltz u. Ewald, Pflüger's Archiv, 1896, s. 389.

[3] Systeme Nerveux, Tome ii., p. 144. Paris, 1858. Liquides de l'Organisme, Tome i., p. 312.

[4] Vulpian, op. cit., p. 158.

[5] Eckhard, Untersuchungen uber die Erection des Penis beim Hunde, Beitrage zur Anat. u. Phys., Abhand. vii. Giessen, 1862.

its secretory activity being increased more blood would flow to the part, and the vessels would dilate. Unfortunately, however, for this hypothesis, in the absence of all secretion, as in the case of an animal poisoned with atropine, the vessels of the tongue will still dilate if the chorda-tympani be stimulated. Another explanation, a too common one when physiological phenomena remain unexplained, is that of inhibition, it being held that vaso-dilator nerves inhibit or paralyze the vaso-constrictor nerves. Apart, however, from the fact that the dilatation of an artery following stimulation of a vaso-dilator nerve is greater than that following paralysis of the vaso-constrictor nerve, to say that the one nerve inhibits the other is rather another way of stating the fact to be explained than an explanation of it. Whatever value may be attached to the explanations offered, whether they be accepted or not, nevertheless, there can be no question as to the fact of there being vaso-dilator as well as vaso-constrictor nerves, and that in all probability they emanate from a focus or center close to the vasomotor or constrictor one, already described, if not actually in the latter.

The conditions favoring vaso-dilator phenomena differ in many respects from those favoring vaso-constrictor ones. Thus the vaso-dilator nerves respond more quickly to stimuli than the vaso-constrictor ones, cold and single induction shocks excite the vaso-dilator nerves, heat and rapidly repeated induction shocks excite the vaso-constrictor nerves, the latent period of the vaso-dilator nerves is longer than that of the vaso-constrictor ones. These differences are of practical importance, since by bearing them in mind the experimenter is enabled to determine whether a nerve contains vaso-constrictor or vaso-dilator fibers or both as obtains, for example, in the case of the sciatic nerve. The vaso-constrictor or vaso-dilator nerves can be excited reflexly as well as directly. Thus, as first shown by Brown-Séquard [1] and Tholozan, if a thermometer be held in one hand and the other hand surrounded by ice or very cold water, in a very short time the temperature of the hand holding the thermometer will fall, the general temperature of the body, however, remaining unaffected, an effect which can only be explained on the supposition that the impression due to the cold is transmitted by the sensory nerves to the spinal cord and thence reflected by the vaso-constrictor nerves to the vessels of the hand holding the thermometer. For the same reason, according to Brown-Séquard,[2] if one foot be immersed in water at about 5° C. (41° F.) the temperature of the other foot will fall in a few minutes perhaps 3.8° C. (7° F.). It has also been shown by Vulpian [3] that if the sciatic nerve be divided, as in a dog, for example, and the central end stimulated, not only the vessels of the limb contract, but also almost all the vessels of the body, the under surface of the tongue even becoming pale through constriction of its vessels. The same

[1] Journal de Brown-Séquard, 1858, Tome i., p. 497.
[2] Ibid., p. 502. [3] Op. cit., p. 237.

reflex effect can also be induced by stimulation of almost any of the sensory nerves, of the posterior roots of the spinal nerves, by irritation of the skin and even by impulses set up in the blood vessels themselves. As illustrations of reflex vaso-dilator action may be mentioned the dilatation of the internal saphenous artery following stimulation of the central cut end of the dorsal nerve of the foot, and the dilatation of the vessel of the ear, brought about through excitation of the central end of the auriculo-temporal nerve, or through stimulation of the central end of the sciatic nerve.

From the well-known fact that stimulation of an afferent nerve causes reflexly sometimes constriction and at other times dilatation of the blood vessels, it is inferred by many physiologists that special reflex constrictor or "pressor nerves" exciting the vasomotor center and causing a rise in blood pressure and special dilatus or "depressor" fibers inhibiting it and causing a fall in blood pressure may run in the same nerve. Among such depressor fibers may be mentioned the depressor nerve of the rabbit whose influence upon the circulation has already been mentioned.

We have already seen that through the contractions and dilatations of the cutaneous blood vessels the blood either remains in the deeper portions of the skin, or comes to the surface of the body, the heat produced in the body, in the one case being retained within it, and in the other lost by either radiation, conduction, etc., and that the application of cold to the general surface so constringes the cutaneous blood vessels that the blood does not rise to the surface, the heat thereby being retained, which would otherwise be lost. That this effect is due to the impression made by the cold being transmitted by the sensory nerves to the spinal cord, and thence reflected by the vaso-constrictor nerves to the cutaneous blood vessels, is shown by the fact of a curarized hot-blooded animal losing this compensating power, through which the heat of the body is normally retained, even though the latter be exposed to cold, the temperature of the curarized animal not being a constant one, but, like that of the cold-blooded one, varying within narrow limits with the temperature of its surroundings.

While the functions that we have attributed to the sympathetic nerve are those possessed by that of animals, there is no doubt that the functions of the sympathetic in man are essentially the same. The blush and pallor due to emotion are familiar examples of reflex vasomotor actions in man. A number of cases have been now recorded by J. W. Ogle,[1] Panas,[2] Verneuil,[3] Trelat,[4] Poiteau,[5] W. Ogle,[6] Bartholow,[7] Seeligmuller,[8] Nicati,[9] Eulenberg,[10] in which

[1] Med.-Chir. Trans., Vol. xli., p. 397.
[2] Mem. de la Soc. de Chirurgie, 1864, T. vi., p. 383.
[3] Bul. de la Soc. de Chirurgie, 1864, 2d serie, T. v., p. 167.
[4] Gaz. des hôpitaux, Paris, 2 Juin, 1868.
[5] Thèse de Paris, 1869, No. 2.
[6] Med.-Chir. Trans., Vol. lii., p. 150. London, 1869.
[7] Quarterly Journal of Psych. Medicine, Vol. iii., p. 134. New York, 1869.
[8] Berlin. klin. Wochenschrift, 1872, No. 2.
[9] La paralysie du nerf sympathetique. Lausanne, 1873.
[10] Berlin. klin. Wochenschrift, 1869, s. 287.

rise of temperature, unilateral sweating of the neck and head, hyperæmia of the conjunctiva, contraction of the pupil, were all observed more or less in consequence of paralysis of the sympathetic due to pressure exerted by aneurisms, tumors, etc., while, according to Vulpian,[1] lesions of the spinal cord may be localized from the vascular dilatation developed in the upper extremities as a consequence of the injury to the vasomotor nerves arising from it. It may also be mentioned in this connection that before most of these observations had been made, Wagner[2] had noticed that, in the case of a decapitated woman, powerful galvanization of the sympathetic caused dilation of the pupil.

While the scope of this work does not permit of a detailed account of the influence exerted by the sympathetic nervous system upon nutrition, it will have been seen, no doubt, from what has been already said, that its influence must be very great, since the amount of blood distributed to the stomach, intestine, liver, kidney, etc., is regulated by the vasomotor nerves. The reflex flow of the alimentary secretions in response to the excitement developed through the presence of food, their natural stimulus, the great vascularity of the liver, spleen, pancreas, during digestion, is brought about through the influence of the sympathetic nerves distributed to these organs. The rapidity and extent with which the absorption of the digested food takes place depends largely upon the condition of the portal circulation, as influenced by the vasomotor nerves, and more particularly by the splanchnic. The circulation of the blood, as we have already seen, is modified by the combined effects of the depressor and vasomotor nerves. It is also through the intermediate action of the latter that the cerebro-spinal centers, more especially those of the medulla, influence the biliary and glycogenic functions of the liver and the secretion of urine by the kidneys. That the amount of blood circulating through the latter, and therefore the amount of urine secreted, is influenced by the vasomotor nerves has already been shown by means of the oncometer by which it will be remembered that the volume of the kidney on the living animal can be shown to vary with the blood circulating through it, the amount of the latter being regulated by the vasomotor nerve.

It may be mentioned in conclusion that, while vasomotor nerves have not as yet been demonstrated in the brain, it is highly probable that such exist. Vasomotor phenomena, however, are produced by impulses emanating from the brain as from other parts of the body peripheral to the vasomotor center.

[1] Op. cit., p. 195. [2] Journal de physiologie, Tome iii., p. 175. Paris, 1860.

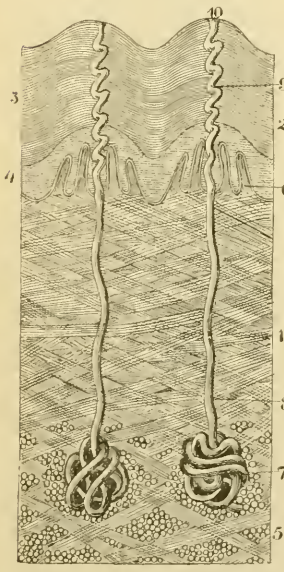
CHAPTER XXXVI.

THE SKIN AND ITS APPENDAGES. SEBACEOUS MAMMARY AND SUDORIFEROUS GLANDS. PERSPIRATION, TACTILE AND OTHER FORMS OF CUTANEOUS SENSATION.

The Skin.

THE skin or integument (Fig. 397) constitutes a general protective and sensory covering for the surface of the body. In addition to these important functions in eliminating the sweat, carbon dioxide, urea, etc., the skin acts also as an excretory organ, supplementing, in this respect, the action of the lungs and kidneys. As we have already seen, the skin, too, in a great measure regulates the production and distribution of heat. To a certain extent, also, the skin acts as an absorbing surface. Further, through special modifications of its sensory structure, the skin ministers to the sense of touch and other forms of cutaneous sensation. The skin, in addition, then, to being sensory and protective, possesses, as well, excretory, calorific, absorbing, and tactile functions. The general appearance of the skin, its extensibility, flexibility, elasticity, and color are sufficiently familiar to all. It may be mentioned in this connection, however, that the color of the skin in the different races of mankind and the varieties of complexion observed in different individuals of the same race, are due to the amount of pigmentary matter present in the deeper layers of the epidermis and that the color of the true skin, or dermis, is whitish and semi-transparent, its apparent pinkish color being due rather to that of underlying parts and the blood circulating through the latter. The furrows and folds of the skin are caused partly by the muscles and joints and partly by loss of elasticity in the skin itself and by the deposition in it of fat. Faint, irregular lines are also observed on most parts of the surface of

FIG. 397.



Vertical section of the skin of the forefinger across two of the ridges of the surface, highly magnified. 1. Dermis composed of an intertexture of bundles of fibrous tissue. 2. Epidermis. 3. Its cuticle. 4. Its soft layer. 5. Subcutaneous connective and adipose tissue. 6. Tactile papillæ. 7. Sweat glands. 8. Duct. 9. Spiral passage from the latter through the epidermis. 10. Termination of the passage on the summit of ridge. (LEIDY.)

the skin, upon the palms of the hand and soles of the feet and particularly upon the palmar surface of the last phalanges; these lines are well marked in the latter situation, being disposed as concentric curves depending upon the regular arrangement of the underlying papillæ of the true skin or dermis. According to Sappey,[1] the cutaneous surface, on the average in man, is equal to about 1.5 square meters (16 square feet), though in men above the ordinary size it may amount to as much as 2 square meters (21.4 square feet). The significance of such variations physiologically will become apparent presently when we consider the excretory functions of the skin.

In harmony with the protective functions of the skin, its thickness varies very much in different parts. Thus, where naturally exposed to constant pressure and friction, as on the soles of the feet or the palms of the hands, the skin, as we shall see, is much thicker than that of the face, eyelids, etc.

The skin consists of two layers, the dermis and epidermis, special modifications of the latter constituting the hair and nails, the sebaceous, mammary, and sweat glands. The dermis, or true skin, also known as the cutis, vera, corium, etc. (Fig. 397), constituting the deeper layer of the skin, is more or less closely connected to the underlying parts by the connective tissue of the adipose layer of the superficial fascia, or when the adipose layer is absent, by the loose connective tissue to the deeper layer of the fascia or subjacent structure, thereby allowing the skin a certain amount of movement backward and forward. The thickness of the adipose layer varies very much in different individuals and in different parts of the same individual. Thus while there is no fat beneath the skin of the eyelids, the upper and outer part of the ear, the penis, and the scrotum, a layer about 2 millimeters ($\frac{1}{12}$ of an inch) in thickness is usually present beneath the skin of the cranium, the nose, the neck, the knee and elbow, and the dorsum of the hand and foot; the adipose layer, on an average, in other situations, measuring from 4 to 12 millimeters ($\frac{1}{6}$ to $\frac{1}{2}$ of an inch). In fat persons, however, it may attain a thickness of 25 millimeters (1 inch) or even more. There is no well-defined line of demarcation between the dermis and the underlying adipose tissue, and after separating the two the dermis looks like a coarsely corded network, the meshes being occupied by small round masses of adipose tissue. The dermis consists principally of a dense intertexture of bundles of fibrous tissue crossing one another at acute angles in different directions, mingled with amorphous matter and some elastic tissue, the latter being most abundant on the front of the body and around the joints. It contains also unstriated muscular fibers, the erector pili muscle, which, passing downward from the more superficial part of the dermis, are inserted into the hair follicles, and which, when excited to contract through the stimulus

[1] Anatomie, Tome iii., p. 564. Paris, 1877.

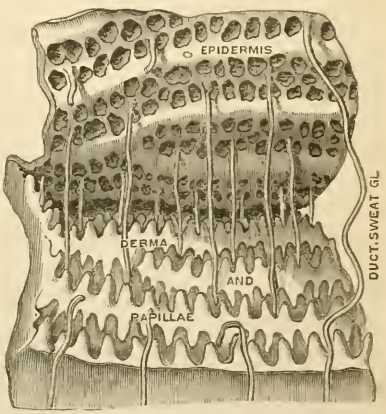
of cold, emotions of fear, or electricity, elevate the hairs and so give rise to the condition known as "goose flesh." In consequence of the gradual transition of the dermis into the subjacent tissues, its exact thickness is difficult to estimate. It may be said, however, to be about $\frac{1}{3}$ of a millimeter ($\frac{1}{72}$ of an inch) thick on the eyelids, about 1 millimeter ($\frac{1}{25}$ of an inch) on the front of the body, and 3 millimeters ($\frac{1}{8}$ of an inch) on the back of the body and the heels, being thickest where the entire skin presents that condition.

The dermis is thinner in the female than in the male, about half as thick in children as in adults and becomes thinner in old age. At its outer surface the dermis is quite dense, being defined by a more homogeneous layer or basement membrane, and projects here and there as small eminences, the papillæ, into the deeper layers of the epidermis. The papillæ, on which the perfection of the skin as an organ of touch largely depends, they being highly developed where the sense of touch is exquisite, and *vice versâ*, are of two kinds, simple and compound, the latter consisting of two, three, or more simple papillæ springing from a common base. The papillæ, composed of a continuation of the fibrous and amorphous structure of the dermis and defined by the basement membrane of the latter, vary in number and size in different parts of the body. They are most numerous and longest in the palms of the hands and soles of the feet, attaining in these situations a length of from $\frac{1}{14}$ to $\frac{1}{5}$ of a millimeter (the $\frac{1}{360}$ to the $\frac{1}{120}$ of an inch), and, being here disposed in double rows on the ridges of the dermis, of which they are the continuation, give rise, as already mentioned, to the curved lines so noticeable on the palmar surfaces of the skin of the last phalanges of the fingers and toes. The papillæ are also quite numerous on the prepuce, glans penis, nymphæ, clitoris, and nipple. In other portions of the body they are less numerous and small, measuring only the $\frac{1}{38}$ of a millimeter (the $\frac{1}{960}$ of an inch). In the face, for example, the papillæ are so little developed as to be hardly recognizable. Most of the papillæ of the palms, fingers, soles, toes, and nipples, especially the compound kind, contain tactile corpuscles in which, as already mentioned, the cutaneous nerves terminate. It will be remembered also that the digital nerves of the fingers and toes appear to terminate in similar shaped, though larger bodies, the Pacinian corpuscles, situated in the subcutaneous tissue and the nerves supplying the skin of the glans penis and clitoris in the Krause corpuscles, resembling the tactile and Pacinian corpuscles, though smaller than either. The dermis with its papillæ is richly supplied with blood vessels and lymphatics, as well as nerves. The arteries penetrating the dermis from beneath end in a capillary network, the latter extending as single loops into the papillæ, while the veins, more numerous and larger than the arteries, terminate in the superficial venous trunks. The lymphatics already referred to are most numerous on the fore and

inner part of the body and limbs, being particularly well developed in the palms and soles. The dermis, consisting largely of white fibrous tissue, is by boiling resolved, in a great measure, into gelatine, the ordinary source of glue, hence also its conversion into leather by tanning. The fibrous structure of the dermis, the papillæ, the mouths of hair follicles, etc., may usually be seen in the cut edge and rough surface of a piece of leather. Deprived of its fatty matters, etc., the dermis, when properly thinned, forms also parchment.

The epidermis, also known as the cuticle or scarf skin, constituting the superficial layer of the skin, bears the same relation to the dermis that the epithelium does to the deeper layer of the mucous membranes. Indeed, the transition of skin into mucous membrane at the mouth and anus is so gradual, that it is impossible to say where one ends and the other begins; in fact, as well known, if the skin be inverted in these places, it becomes mucous membrane, and if the mucous membrane be everted, it becomes skin. The internal surface of the epidermis is applied directly to the papillæ (Fig. 398) of the dermis, and follows closely all their inequalities; its external surface is marked by very shallow grooves corresponding to the furrows between the latter. The epidermis is entirely destitute of blood vessels and lymphatics, deriving its nutritive fluid (like all other vascular parts), by osmosis, from the blood of the dermis. It was for a long time supposed that the epidermis was also without nerves. Modern investigations, however, make it probable that some of the cutaneous nerves pass through the dermis, terminating as non-medullated nerve fibers among the deeper layers of the epidermis in slightly bulbous-like extremities, or in a plexus of fine fibrils. However this may be, impressions made upon the epidermis will be appreciated, whether the latter be provided with nerves or not, being transmitted through pressure to the exquisitely sensitive dermis beneath. The epidermis serves as a protective covering to the soft and delicate dermis, which would be otherwise constantly exposed to laceration and drying.

FIG. 398.



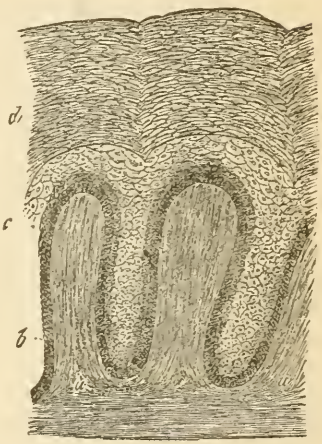
Epidermis elevated so as to show papillæ. (HIRSCHFELD.)

Indeed, if the epidermis be removed, contact of the atmosphere alone will inflame the dermis, which, after death, rapidly dries. The epidermis is therefore thicker in those parts which are most

exposed, as in the palms and soles, where it may measure as much as 2 millimeters (the $\frac{1}{12}$ of an inch or more), being very thin, on the other hand, upon the face, the eyelids, and in the external auditory meatus, attaining in these situations only a size of the $\frac{1}{24}$ to $\frac{1}{36}$ of a millimeter ($\frac{1}{600}$ to the $\frac{1}{900}$ of an inch). The whole skin then, including the dermis, in its thickest part would measure about 5 millimeters (the $\frac{1}{5}$ of an inch). The thickness of the epidermis is, however, dependent to a great extent upon the amount of pressure to which the skin is subjected, being very thick in the palm of the laborer and the sole of the plowman. Corns are thickened portions of the epidermis, and are due to the parts affected being exposed to excessive pressure or friction, hence they are developed not only in the feet by tight shoes, but on the knee of the shoemaker by constant hammering, and in front of the clavicle of the soldier by the pressure of the musket. The pain caused by corns is due to inflammation of the dermis, which they excite by pressing upon its delicate structure, just as any foreign body, a small stone, will do under similar circumstances. The epidermis consists of two layers, the rete mucosum and the cuticle. The rete mucosum or Malpighii, with a thickness varying from $\frac{1}{70}$ to $\frac{1}{3}$ of a millimeter (the $\frac{1}{1700}$ to the $\frac{1}{75}$ of an inch), constituting the deeper internal soft layer of the epidermis, is moulded upon the adjoining surface of the dermis, and when separated by maceration or putrefaction presents impressions corresponding exactly with the papillæ, furrows, depressions, etc., of the latter, the more prominent irregularities of the dermis being, as already mentioned, visible upon the outer surface of the cuticle, but less distinctly. The rete mucosum consists of several irregular layers of cells of different forms, more or less agglutinated together. Those lying next to the dermis are somewhat elongated in figure, varying in length from the $\frac{1}{160}$ to $\frac{1}{80}$ of a millimeter ($\frac{1}{4000}$ to the $\frac{1}{2000}$ of an inch), and disposed perpendicularly, while the succeeding ones are of a rounded form and often marked with ridges and furrows, in sections appearing as spines. As the cells are gradually pushed from below upward through the continual development of new cells at the surface of the dermis, they become more and more flattened, lose their soft, granular contents and nucleus, and, becoming keratose, give rise to the different layers of the rete mucosum, and are finally transformed into the dry, horny scales of the cuticle. While in the white race the cells of the rete mucosum are colorless and like those of the cuticle translucent, allowing the color of the underlying dermis to be seen, in those of the black races, the negro especially, the deeper ones (Fig. 399) are filled with brown or black pigmentary matter, which gives rise to their characteristic dark color, and, when present in smaller quantities, to the various shades of complexion of other races, of different individuals, and of different parts of the skin of the same individual, while the accumulation of this pigmentary matter in

spots causes freckles. As the cells of the deeper layers of the rete mucosum are gradually transformed into those of the cuticle, the pigmentary matter gradually diminishes and finally disappears. It is interesting in this connection to note that the color of the dermis in the negro is the same as that of the white, and that the whole skin of the negro fœtus is as pale as that of the white one. The fact of the pigment being developed in the deep cells of the rete mucosum only at or after birth would indicate that the black race had descended from the white one rather than the reverse. Further, since in the dark races and the semi-burnt ones of the white races, the pigment is developed, not in the superficial, but in the deep layers of the rete mucosum, it is to be inferred that the pigment is eliminated by the cells of the rete mucosum from the blood of the dermis, and that the effect of the heat of the sun in temperate or tropical climates is not to modify directly the color of the skin, but in rendering the liver torpid, to throw upon the skin the elimination of the coloring and other matters of the bile, and, hence, only indirectly affecting it. That such is the case is rendered probable also from the fact of the cutaneous pigment being essentially carbonaceous in nature, as is that of bile. While there is no doubt that the cells of the rete mucosum are gradually transformed into those of the cuticle, they themselves are derived from those of the dermis, since, as we shall see hereafter, the epidermis is derived from the epiblast or external blastodermic membrane of the embryo, and the dermis from the mesoblast or middle blastodermic membrane. Such being the case, it is more probable that the deep epidermal cells of the adult are derived by unbroken descent from the original epiblastic ones of the embryo than from those of its dermal mesoblastic ones.

FIG. 399.

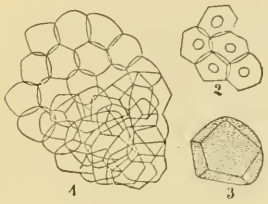


Skin of the negro, vertical section, magnified 250 diameters. *a*, *a*. Cutaneous papillæ. *b*. Undermost and dark-colored layer of oblong vertical epidermis-cells. *c*. Mucous or Malpighian layer. *d*. Horny layer. (KÖLLIKER.)

The cuticle, or cuticula, constituting the most external superficial portion of the epidermis, consists of numerous layers of hard, flattened, nearly dry, yellowish translucent cells, irregularly polygonal in form, generally granular, but without nuclei, measuring from the $\frac{1}{800}$ to $\frac{1}{300}$ of a millimeter ($\frac{1}{20000}$ to $\frac{1}{7500}$ of an inch) in diameter, and composed chemically of keratin, or horny matter; the deeper cells being rather thicker and rounder than those of the superficial layers. As the deeper surface of the cuticle is being continually renewed by fresh cells from the rete mucosum, its free surface is as constantly

worn away, or shed off in flakes, constituting the so-called scurf (Fig. 400) and dandruff (Fig. 401). In many of the lower animals, as in snakes, for example, the cuticle exfoliates from time to time entire. By treating the cuticle with a solution of potash its

FIG. 400.



Scurf from the leg. 1. A fragment of scurf, consisting of dried, flattened non-nucleated cells or scales. 2. A few cells with a nucleus. 3. A cell more highly magnified, to exhibit its polyhedral form.

FIG. 401.

Fragment of dandruff from the head. 1. Portion of dandruff, consisting of non-nucleated cells. 2. Several fragments, consisting of nucleated cells. 3. Isolated cells, some with and without nuclei. 4. A cell more highly magnified, exhibiting granular contents and a nucleus.

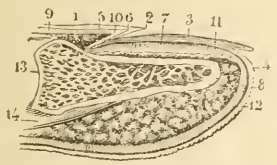
scales separate from one another, swelling up into vesicles; it is for this reason that alkaline solutions remove the epidermis. In tanning, for example, the epidermis is removed by macerating the skin in lime, etc. A blister or burn, in producing inflammation of the dermis and effusion of liquid, breaks up the soft cells of the rete mucosum, and so elevates the cuticle. If the skin be macerated after death, the cuticle, through disorganization of the rete mucosum, detaches itself, and when, under such circumstances, it is thick and strong, as in the case of the hand and foot, it may be stripped off like a glove.

The Nails.

The nails, or ungues, appendages of the skin corresponding to the claws and hoofs of other animals, and situated upon the dorsal surfaces of the distal phalanges of the fingers and toes, not only serve to protect these parts, but are also important as prehensile organs, in civilized races more especially, in the case of the fingers, but in certain barbarous ones, in that of the toes as well. The nails are thin, flexible, translucent, quadrilateral plates, continuous with the epidermis (Fig. 402), with which they are detached if the latter be separated by maceration from the dermis. The nail resting upon the depressed surface of the dermis, known as the matrix, or bed, as described by anatomists, consists of the root, body, and free border. The root is lodged in a deep groove of the matrix, the vallecula unguis, while the lateral borders of the body of the nail fit into rather shallow grooves, the free border of the nail being that part detached from the skin. The color of the nail is due to its translucency, which allows the color of the highly vascular, or underlying dermis, or matrix to be seen; the lunula, or whitish spot at the root, defined by the semicircular line, is due to the matrix being there less vascular. The grooves exhibited more particularly on the under surface of the nail are the impressions made

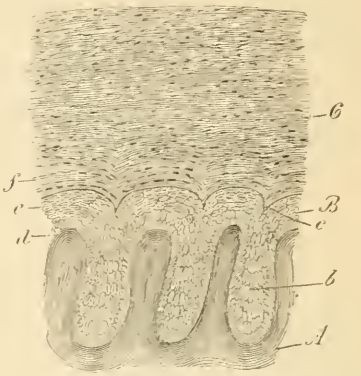
by the fine longitudinal ridges and papillæ of the dermis of matrix upon which the nail is moulded. The nail, like the epidermis, consists of two layers—a horny layer and a soft layer. The soft

FIG. 402.



Vertical section of the end of a finger. 1. Epidermis on the back of the finger. 2. Point at which it is reflected to become continuous with the nail. 3. The nail. 4. Epidermis at the end of the finger. 5, 6, 7, 8. Surface of the dermis corresponding with the position of the soft epidermic layer. 9, 10, 11, 12. Dermis. 13. Last phalanx. 14. Flexor tendon.

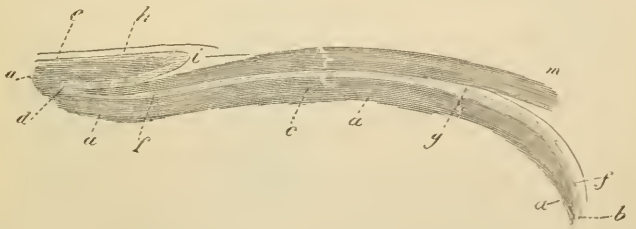
FIG. 403.



Vertical transverse section through a small portion of the nail and matrix, highly magnified. *A*. Corium of the nail bed, raised into ridges, or laminæ; *a*. Fitting in between corresponding laminæ; *b*. Of the nail. *B*. Malpighian, and *C*, horny layer. *d*. Deepest and vertical cells, *e*. Upper flattened cells of Malpighian layer. (KÖLLIKER.)

layer corresponding to the rete mucosum of the epidermis, consists, like the latter, of delicate, polyhedral nucleated cells, which are being continually transformed into the scales of the horny layer. The latter, corresponding to the cuticle of the epidermis, consists of a number of layers of flattened nucleated cells, or scales, but so intimately associated that they can only be recognized under the microscope, after separation from one another by treatment with alkalies, etc. The thickness of the true nail—that is, of its horny layer at the root—is from $\frac{1}{8}$ to $\frac{1}{4}$ of a millimeter ($\frac{1}{200}$ to $\frac{1}{100}$ of an inch), and at the middle of the body of the nail, from $\frac{5}{8}$ to $\frac{5}{6}$ of a millimeter ($\frac{1}{40}$ to $\frac{1}{30}$ of an inch). Through the constant addition of cells, the root of the nails grows in length, and through addition of the cells beneath, in thickness—the free cut edge of the nail consisting of the horny layer only (Fig. 404). The average rate

FIG. 404.



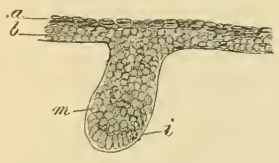
Longitudinal section through the middle of the nail and bed of the nail. *a*. Bed of the nail and cutis of the back and points of the fingers. *b*. Mucous layer of the points of the fingers. *c*. Of the nail. *d*. Of the bottom of the fold of the nail. *e*. Of the back of the finger. *f*. Horny layer of the points of the fingers. *g*. Beginning of them under the edge of the nail. *h*. Horny layer of the back of the fingers. *i*. Ends of it upon the upper surface of the root of the nail. *k*. Body. *l*. Root. *m*. Free edge of the proper substance of the nail. Magnified 8 diameters. (KÖLLIKER.)

of growth of the nails is said to be $\frac{1}{1\cdot\frac{2}{2}}$ of a millimeter ($\frac{1}{3\frac{1}{2}}$ of an inch) per week, and to be more rapid in summer than in winter.[1]

The Hairs.

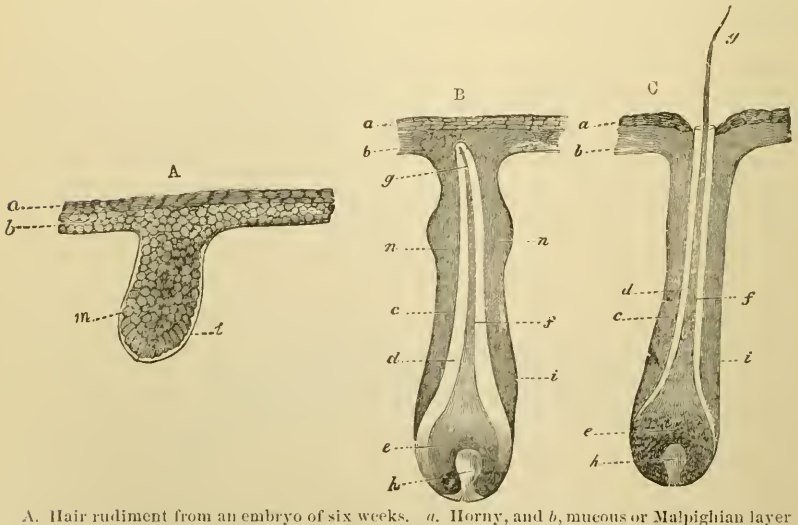
The hairs, or pili, like the nails, appendages of the skin, and more particularly of the rete mucosum of the epidermis, are first noticed at about the third or fourth month of intrauterine life, as little black specks beneath the cuticle, consisting of a mass of cells, defined by a basement membrane (Fig. 405), developed through invagination, or the growing downward of the cells of the rete mucosum into the dermis. As development advances, the cells of which this flask-like body consists are differentiated into a central and a lateral portion (Fig. 406, A), the former the rudiment of the future hair, the latter the root-sheath, or the lining of the hair follicle, while the projecting of the dermis into the bottom of the flask-like hair forms its papillæ. With the gradual upward growth of the hair and the development of the different parts, of which, as we shall see, it consists (Fig. 406, B, C), the root-sheath

Fig. 405.



Rudiment of the hair from the brow of a human embryo, sixteen weeks old, magnified 350 diameters. *a*. Horny layer of the epidermis. *b*. Its mucous layer. *i*. Structureless membrane surrounding the rudiment of the hair, and continued between the mucous layer and the corium. *m*. Roundish, partly elongated cells which especially compose the rudiments of the hair. (KÖLLIKER.)

Fig. 406.



A. Hair rudiment from an embryo of six weeks. *a*. Horny, and *b*, mucous or Malpighian layer of cuticle. *i*. Basement membrane. *m*. Cells, some of which are assuming an oblong figure, which chiefly form the future hair. B. Hair rudiment, with the young hair formed, but not yet risen through the cuticle. *a*. Horny layer. *b*. Malpighian layer of epidermis. *c*. Outer, *d*, inner root sheath. *e*. Hair-knob. *f*. Stem, and *g*, point of the hair. *h*. Hair-papilla. *n*, *n*. Commencing sebaceous follicles. C. Hair-follicles with the hair just protruded. (KÖLLIKER.)

[1] Quain's Anatomy, 1878, Vol. ii., p. 219.

divides into the inner and outer root-sheaths, the former, except at the bottom, subdividing into Huxley's and Henle's layers, the latter surrounded and defined by a fibrous membrane derived from the dermis, constituting the wall of the hair follicle.

Finally, the hair, being fully formed, penetrates the cuticle, the papilla to which it is attached having been provided with nervous filaments and capillary blood vessels. The hair is usually described as consisting of a root beginning in the skin as a club-like expansion, the bulb and a shaft or stem projecting from the skin, and terminating in the end or point. It is composed (Fig. 407) usually of a medulla, or central axis, around which are concentrically disposed the cortical substance and cuticle. The medulla consists of cuboidal cells, having a diameter of from the $\frac{1}{80}$ to $\frac{1}{48}$ of a millimeter ($\frac{1}{2000}$ to $\frac{1}{1200}$ of an inch), with granular contents, and an indistinct nucleus, usually intermingled with small bubbles of air, which have penetrated from the ends of the hair, and, when present, giving rise to the white silvery luster of the latter. In downy hairs the medulla is absent. The cortical substance, or the cortex, constitutes the chief bulk of the hair, and is that part upon which the color of the hair principally depends in different individuals and races. It is composed of several layers of flexible fibers, the latter consisting of elongated fusiform cells. With the loss of the coloring matter, which is generally diffused through the cortical substance, the latter becomes white. The cuticle consists of a single layer of thin, colorless, quadrilateral cells, overlapping each other like the shingles of a roof. The edges of these scales being directed upward and outward along the shaft offer an obstacle to any movement of the hair otherwise than with its root forward when rubbed between two surfaces. It is upon this fact that the felting of hair and wool of various animals depends. The hair, like the epidermis, being destitute of blood vessels, derives its nutritive liquid by osmosis from the blood of the vessels of the papilla. While analogy would lead one to suppose the nerve filaments of the papilla penetrate the hair, as a matter of fact, no nervous filaments having as yet been demonstrated in it, any sensibility that the hair may possess must depend, therefore,

FIG. 407.

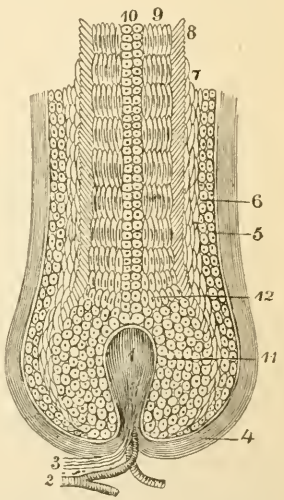


Diagram of structure of the root of a hair within its follicle. 1. Hair papilla. 2. Capillary vessel.—3. Nerve fibers. 4. Fibrous wall of the hair follicles. 5. Basement membrane. 6. Soft epidermis, lining of the follicle. 7. Its elastic cuticular layer. 8. Cuticle of the hair. 9. Cortical substance. 10. Medullary substance. 11. Bulb of the hair composed of soft polyhedral cells. 12. Transition of the latter into the cortical substance, medullary substance, and cuticle of the hair. (LEIDY.)

upon that of the papilla which the hair bulb tightly encloses or caps. The hairs are continually renewed by constant growth. In some instances, especially after disease, they are cast off or shed, new ones being produced. Permanent baldness is due to atrophy of the papillæ, while the sudden blanching of the hair, occurring sometimes in a single night, is due to the greater part of the medulla and cortex becoming filled with air.[1]

Chemically, hairs are composed of fats, a gelatine-like substance, albuminous matters, containing a large proportion of sulphur, peroxide of iron, traces of manganese, silica, sodium, and potassium chlorides, calcium sulphate and phosphate, and magnesium sulphate.[2] With the exception of the palms of the hands and soles of the feet, the palmar surface of the fingers and toes, the lips, lining of the prepuce and glans penis, hairs cover nearly every part of the surface of the body. The hairs generally project obliquely from the skin, and are regularly disposed, usually in curving lines from particular points. They differ very much as regards their size, fineness, color, form, and number, in different races, sexes, individuals, and parts of the body. Of the long hairs, attaining sometimes in women a length of 90 cm. (three feet) or more, and a diameter of from the $\frac{1}{60}$ to $\frac{1}{16}$ of a millimeter ($\frac{1}{1500}$ to $\frac{1}{400}$ of an inch), the finest are found upon the head. The short, stiff hairs of the nostrils and edges of the eyelids, are from the $\frac{1}{16}$ to $\frac{1}{7}$ of a millimeter ($\frac{1}{400}$ to the $\frac{1}{170}$ of an inch) in diameter, the fine downy ones from the $\frac{1}{80}$ to $\frac{1}{60}$ of a millimeter ($\frac{1}{2000}$ to the $\frac{1}{1200}$ of an inch). While the fine silken hair of the head in the white race is cylindrical, the crisp hair of the head and beard of the negro is more or less flattened cylindrical. It has been estimated[3] that upon a square inch of scalp there are about 1,000 hairs, the number upon the entire head amounting to 120,000. The hairs are elastic, readily electrified by friction, especially in cold, dry weather, and very hygrometric. The latter property is taken advantage of in the making of delicate hygrometers, the hair elongating through the absorption of moisture. The hairs not only serve to protect the general surface, as in shielding the head from excessive cold or heat, but also guard certain orifices, as those of the ears and nose. The eyebrows prevent the perspiration from the forehead running on to the lids, the eyelashes the surface of the conjunctiva from dust, etc. Hair, being a bad conductor of heat, serves also to retain that produced within the body. It has already been mentioned that the hairs are quite regularly disposed, and it will be further observed that if a man assume a crouching attitude, with elbows upon the knees, and the chin resting upon the hands, that their general direction upon the extremities is obliquely downward, a disposition such, that if the person be exposed to wet weather, the rain

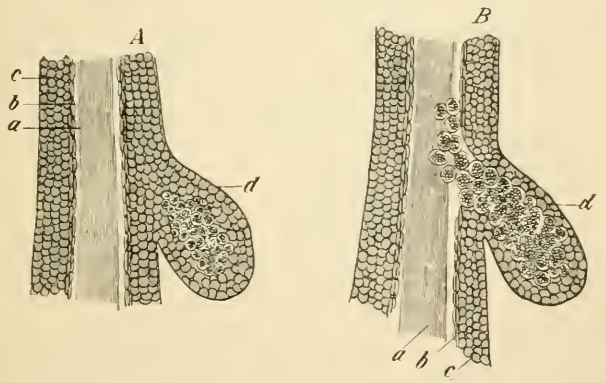
[1] Landois, Virchow's Arch., 1866, Band xxxv., s. 375. Wilson, Proc. Roy. Soc. Lond., 1867, Vol. xv., p. 406. [2] Quain's Anatomy, Vol. ii., p. 226.
[3] Wilson, Healthy Skin, p. 84. Philadelphia, 1854.

will be drained off, an effect obviously of advantage to the primitive man, as well as to those who go naked at the present day. Finally, the hairs may be regarded, to a certain extent at least, as so many excretory organs, since their growth necessarily involves the excreting from the blood the different principles of which we have seen that they chemically consist, and which, if retained within the system, in all probability would give rise to disease.

Sebaceous Glands.

The sebaceous glands, like the nails and hair, are appendages of the epidermis, being developed during the fourth and fifth months of intrauterine life as outgrowths of the hair follicles, into which, with but few exceptions, they eventually open. Each sebaceous gland begins (Fig. 408, *A*) as a solid bud sprouting out into the

A FIG. 408. *B*



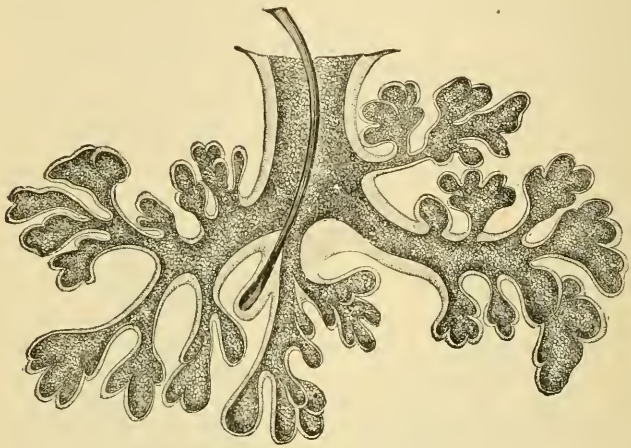
The development of the sebaceous glands in a six months' fœtus. *a*. Hair. *b*. Inner root-sheath, here more closely resembling the horny layer of the epidermis. *c*. Outer root-sheath. *d*. Rudiments of the sebaceous glands. *A*. Flask-shaped rudiments of the gland, with fat developed in the central cells. *B*. Larger rudiments. (KÖLLIKER.)

dermis from the external root-sheath of the hair follicle, and consists entirely of nucleated cells. As development advances, however, the cells in the central portion of the flask-like (Fig. 408, *B*) bud develop fat, which gradually extending themselves, penetrate the root-sheaths of the hair follicle, and so pass into the cavity of the latter as the primitive sebaceous secretion, while through the further division and subdivision of the primitive bud the latter assumes the form of a simple or compound alveolar gland. The sebaceous gland when fully developed consists of a delicate wall of fibrous tissue defined by a basement membrane lined with an epithelium consisting of polyhedral nucleated cells, with granular contents, the cavity of the gland being filled with sebaceous matter. The latter or the sebum, consists of water, epithelium, olein and palmatin, soaps, cholesterin and inorganic salts, principally insoluble earthy phosphates and alkaline chlorides. The sebum, somewhat

modified, constitutes the smegma præputii, the vernix caseosa of the newborn child, the meibomian secretion of the eyes, and, when mixed with that of the sweat glands of the ear, the cerumen, or ear wax.

The sebaceous glands are very numerous, existing almost everywhere, except in the palms and soles. Usually associated with the hair follicles (Fig. 409), they are disposed around the latter in

Fig. 409.



A large gland from the nose, with a little hair-sac opening into it; magnified fifty diameters. (Kölliker.)

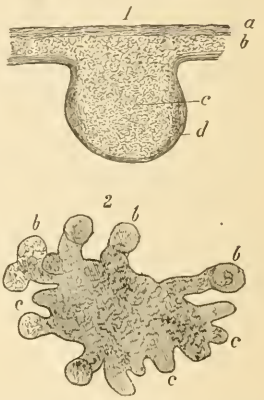
groups varying from two to eight to each follicle, and imbedded in the more superficial part of the dermis, appearing as round whitish bodies, and measuring on an average from $\frac{1}{4.8}$ to $\frac{1}{2}$ of a millimeter ($\frac{1}{120}$ to $\frac{1}{50}$ of an inch) in diameter. The largest sebaceous glands are those of the nose, concha of the ear, skin of the penis, the scrotum, labia, and areola surrounding the female nipple.

The use of the sebaceous matter is to smear the hairs with oil as they grow out of the skin and thoroughly to imbue the cuticle with the same, through which it is rendered repellant of water. The greasiness of the skin thus produced is the cause of smut and dirt adhering to the person so readily and necessitating the use of soap for the removal of the same. The too free use of alkaline washes, however, in depriving the cuticle of its natural oil, renders the skin dry and harsh. The sebaceous matter often becoming inspissated, distends the glands producing it, especially in those of the nose, and becoming incorporated at the mouth of the duct with dirt if squeezed out is often regarded on account of the shape as a worm, the dirt being supposed to be the head. It should be mentioned, however, that the sebaceous matter frequently contains the so-called pimple mite, the Acarus or Demodex folliculorum.

Mammary Glands and Milk.

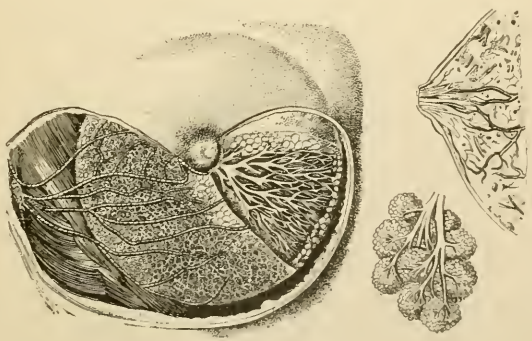
The mammary, like the sebaceous glands just described, are also appendages of the epidermis, being developed in the fourth or fifth month of intrauterine life (Fig. 410, 1, 2) as solid invaginations or projections of the rete mucosum into the dermis, the latter furnishing the dense layer investing them. As development advances each primitive gland gives off a number of buds, the future lobes, numbering at birth from twelve to fifteen, which, through continued division and subdivision into lobules, and the latter into acini or secreting vesicles, ultimately assume the constitution of a gland (Fig. 411), such as the parotid or submaxillary, the whole, however, being so closely associated by connective tissue as to give the appearance of being homogeneous rather than lobulated. Just before the ducts from the lobes reach the nipple they expand beneath the areola into the so-called lactiferous sinuses, especially observable in the human female during lactation, and constituting the large milk reservoirs in the cow. As the lacteal or galactophorous ducts from each lobe terminate at the summit of the nipple in a small orifice, the number of the latter, usually twelve to fifteen, correspond with the

Fig. 410.



Development of the lacteal gland. 1. Rudiment of the gland in a male embryo, at five months. *a*. Horny layer. *b*. Mucous layer of the epidermis. *c*. Process of the latter or rudiment of the gland. *d*. Fibrous membrane around the same. 2. Lacteal gland of a female fœtus, at seven months, seen from above. *a*. Central substance of the gland, with larger (*b*) and smaller (*c*) solid outgrowths, the rudiments of the large gland lobes.

Fig. 411.



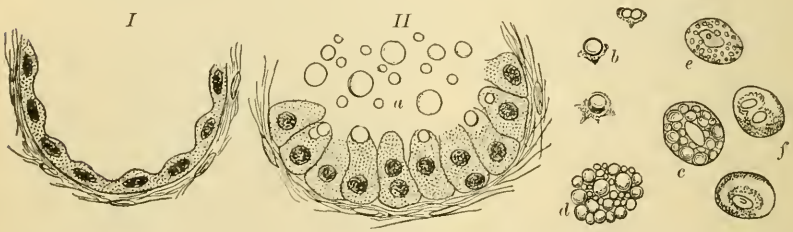
Mammary Gland, Acini, and Ducts.

number of lobes. The mamma, as a whole, is of a firm consistence; of a pinkish-white color, of circular form with its ex-

ternal surface convex and prolonged to the nipple. The latter, provided with sensitive papillæ, is highly vascular and capable of erection. The nipple, reddish or brownish, is surrounded by an areola of skin usually of the same color, and containing sebaceous glands appearing as whitish eminences, which, during sucking, secrete a fatty substance which protects the part from excoriation. The mammæ exist in the male, but usually only in a rudimentary condition. Their presence in animals gives rise to the name mammalia, the highest order of vertebrates, and while, as a general rule, they are attached in such to the abdominal walls, in man, monkeys and the elephant, they are situated on the anterior part of the thorax.

It has been shown by modern investigations[1] that while the secreting cell of the mammary gland during the inactive period (Fig. 412, *I*) are polyhedral, flat, and uninucleated, they become during the active period (Fig. 412, *II*) cylindrical, tall, and multinucle-

FIG. 412.



I. Inactive acinus of the mamma. *II.* During the secretion of milk—*a*, *b*, milk-globules; *c*, *d*, *e*, colostrum corpuscles; *f*, pale cells (bitch). (LANDOIS.)

ated and finally disintegrate their contents, forming the milk. The secretion of the mammary glands or milk, having a specific gravity of from 1.026 to 1.035 and constituting a perfect emulsion, consists of a colorless liquid, the milk plasma, and innumerable fat-like bodies, the milk corpuscles, or globules. The latter, to which the opaque, whitish color of milk is due, are very variable in size, $\frac{1}{480}$ to $\frac{1}{50}$ of a millimeter ($\frac{1}{12000}$ to the $\frac{1}{1250}$ of an inch), and consist of minute drops of fat surrounded apparently by a thin film of casein, the so-called "paptogen" membrane.

Milk is composed in one hundred parts in round numbers of: Water, 88.58; proteids, 3.69; fat, 3.52; lactose, 4.29; salts, 0.16.[2] The proteids of milk are casein, lactalbumin, and lactoglobulin, the two latter occurring, however, in much smaller quantities than the casein. The fat consists chiefly of stearin, palmitin, and olein, with small amounts of butyric and caproic acids and of small quantities of cholesterin, lecithin, and a yellow pigment. The salts consist of sodium and potassium chloride, potassium,

[1] Heidenhain, in Hermann, Handbuch, Bd. v., 1883, s. 381.
[2] Halliburton, op. cit., p. 577.

calcium, magnesium, and ferric phosphate, sodium and potassium sulphate, and traces of silica. With the exception of the water and salts the constituents of the milk are elaborated by the cells of the mammary gland out of materials supplied by the blood, they not existing as such in the latter. That the fat of the milk is not derived exclusively from the fat of the food is shown by the fact that the milk of a bitch fed upon a purely flesh diet contains larger amounts of fat—the albumin splitting, as already mentioned, into a nitrogenous (urea) and non-nitrogenous molecule (fat). That the salts of the milk even are not derived from the blood by a mere process of filtration, but are elaborated by the cells of the gland, is shown by the fact of the amount in which they are present in the two fluids being so different. The quantity of milk secreted in twenty-four hours varies very much, depending upon the condition of the female, kind of food, etc. Perhaps it may be said that the daily production of milk by the human female amounts to about one liter or nearly a quart. The gases of human milk have not been investigated; that of the cow contains in 100 volumes: Nitrogen, 1.41; oxygen, 0.16; carbon dioxide, 0.72.

The milk formed at the beginning of lactation—the colostrum—differs from the later in having a higher specific gravity, in being thinner, yellowish in color, and containing many of the milk cells in an entire condition.

During the intervals of lactation the mammary glands secrete only a small quantity of viscid mucus.

The secretion of milk appears to be influenced if not controlled by the central nervous system through vasomotor or secretory nerves.[1] It is well known to obstetricians that the milk of a woman affected by some strong emotion or attacked by disease will not only be altered in quality but even suppressed altogether. The results of experiments made upon animals, though conflicting in some respects, confirm upon the whole the above view, division of the spermatic nerve being usually followed by an increased flow of milk, stimulation by a diminished one. The effect is probably due to vasomotor action, though according to one observer secretory fibers have been traced directly to the cells of the mammary gland.[2] From the fact, however, that after the severance of all nervous connections milk is still secreted, it may be inferred that the mammary gland acts automatically, even though influenced by the central nervous system.

Sudoriferous Glands.

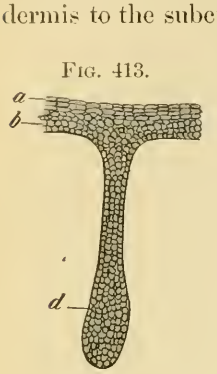
The sudoriferous or sweat glands, like the sebaceous and mammary glands, are appendages of the epidermis, beginning about the fifth month of intrauterine life as flask-like involutions of the cells of the

[1] Heidenhain in Hermann's Handbuch, Band v., Thl. 1, s. 392. Rohrig, Virchow's Archiv, Band 67, 1876, s. 119. Eckhard, Beiträge, 1855, s. 12, 1877, s. 117. Mironow, Archives des Sciences biologiques, St. Petersburg, Tome iii., 1894, p. 353.

[2] Arnstein, Anat. Anzeiger, Band x., 1895, s. 410.

rete mucosum of the epidermis into the dermis (Fig. 413). As development advances this solid flask-like rudiment becomes transformed into a hollow tube, which, extending itself through the dermis to the subcutaneous adipose tissue, terminates at the one end in a coil, and at the other end as the sweat pore on the surface of the skin, a passage-way in the meantime being formed in the epidermis leading from the latter into the hollow tube. Each sweat gland, when fully formed, consists of a tube convoluted at its commencement, the secreting portion of a yellowish-red color, spheroidal in form, with an average diameter of 1.2 millimeters (the $\frac{1}{20}$ of an inch), and passing thence upward, as the sweat duct, in a slightly tortuous manner to the external surface of the dermis. The tube consists of an external fibrous layer, succeeded by a basement membrane, the latter supporting an epithelium of polyhedral nucleated cells containing granular and yellowish pigment matter. As just mentioned, at the point where the sweat duct opens on the surface of the dermis a passage-way is continued through the epidermis to the exterior. Where the epidermis is thin the passage-way is straight, but where thick, as in the palms and soles, it takes a spiral course, terminating at the surface in a funnel-shaped orifice. The openings of the sweat ducts may be distinctly seen disposed in a single row on the summits of the ridges of the skin of the palms and soles, if the latter be viewed with a common pocket lens. In other situations, however, they are far less apparent. With the exception of the concave surface of the concha of the ear, the glans penis, the inner layer of the prepuce, and perhaps a few other places, the sweat glans are found in every part of the skin. The number varies, however, very much according to the part of the skin examined. Thus, while according to Krause,[1] in the palmar surface of the hand there may be as many as 2,736 sweat glands in 6.7 sq. cm. (1 square inch) of skin, in that of the nates there may be as few as 417 per sq. cm. It is this variation in the number of sweat glands existing in different parts of the skin that renders any determination as to their total number, as estimated, for example, by Krause at 2,381,248, so very uncertain. Assuming that the secreting portion of the coil of each sweat duct, when unravelled, measures 1.5 millimeters ($\frac{1}{16}$ of an inch) in length on the above estimate, if the tubes were placed end to end they would extend a distance of 3.8 kilometers ($2\frac{1}{3}$ miles). It should be mentioned, however, with reference to this last estimate, that the length of the excretory portion of the duct is not taken into consideration, which

FIG. 413.



Rudiment of a sudoriparous gland of a human embryo at five months; magnified 350 diameters. *a*. Horny layer of the epidermis. *b*. Mucous layer. *c*. Corium. *d*. Rudimentary glands, as yet without any cavity, and consisting of small round cells.

[1] Wagner, Physiologie, Band ii., s. 131. Braunschweig, 1844.

will depend on the thickness of the skin. Supposing the latter to be 5 millimeters ($\frac{1}{5}$ of an inch), the mean of its thickest and thinnest parts, the total length of the excretory portion of the sweat ducts would amount to 12.5 kilometers (7½ miles), a somewhat exaggerated estimate, and very approximate, it must be admitted. The sweat glands, somewhat modified, constitute the ceruminous glands of the ear, which will be referred to again in our account of that organ, and also the odoriferous glands of the axilla.

In the latter situation they form a patch in the subcutaneous connective and adipose tissue often an inch and a half or more in diameter, being largest in the center of the patch and gradually diminishing toward the circumference, where they become undistinguishable from the ordinary sweat glands. The odoriferous glands of the axilla not only secrete sweat but a strongly odorous substance, hence their name, which varies somewhat in character in the different races of mankind. Indeed, it is to this secretion that the peculiar odor of negroes is to a great extent to be attributed, the glands as a general rule being better developed in the negro than in the white man, attaining in the former the size of a pea.

Perspiration.

The secretion of the sudoriferous or sweat glands, the perspiration or sweat, although being continually elaborated by the latter from the blood, does not always appear as such upon the surface of the skin, passing from the body in the form of an insensible vapor as rapidly as produced. If, however, through the amount of the sweat secreted being increased, or from the condition of the atmosphere, as regards temperature and moisture, the evaporation of the sweat is prevented, the sweat remains in the form of minute drops, and constitutes what is commonly understood as sweat or perspiration. There is no difference, therefore, between the insensible and sensible perspiration, the form in which it may be exhaled, whether as liquid or vapor, depending simply upon the conditions just mentioned.

Sweat is a clear watery liquid, of a specific gravity of 1.003 to 1.004, having a saline taste and a peculiar odor according to the part of the skin from which it is obtained. The reaction of the sweat appears to be acid, though, according to many observers, it is alkaline, the acidity being due to the latter, to the admixture of fatty acids derived from the sebum.[1] Sweat consists of more than nine-tenths water, the remaining constituents being salts, fats, urea, and other organic matters in traces, and epithelium.[2] The inorganic salts consist principally of sodium chloride, 0.2 to 0.3 per cent., though alkaline sulphates and phosphates are present in small quantities. The fatty matters, amounting to 0.4 per cent. are produced by the sebaceous glands. Urea is usually present only in small quantities, 0.08 per cent. It may be mentioned, in this connection,

[1] Hammarsten, op. cit., p. 327. [2] Charles, Physiological Chemistry, p. 349.

that of the carbon dioxide eliminated by the system about $\frac{1}{50}$ to $\frac{1}{200}$ is exhaled by the skin together with the sweat.

So far as known to the author, the celebrated Sanctorius was the first to endeavor to determine experimentally, during the seventeenth century, the amount of the perspiration. The method made use of was to weigh daily the body, and all the solid and liquid ingesta and egesta, and from the loss of weight experienced by the body, to deduce the amount of vapors transpired. Thus, if from every 8 pounds of ingesta taken in 24 hours there were 3 pounds of sensible egesta (44 ounces urine, and 4 ounces feces), it was inferred that the remaining 5 pounds of ingesta passed from the body insensibly in the form of vapor. Unfortunately, however, as the latter included the vapor exhaled from the lungs as well as that from the skin, and the observations being simply embodied as aphorisms,[1] no numerical tables given, the results obtained have now but little value, although Sanctorius experimented daily in the manner described for a period of thirty years. Although numerous and interesting observations and experiments were made during the eighteenth century by Dodart, Keill, Rye, Gorter, Lining, Hales, Stark, with a view of determining the amount of the perspiration and the conditions affecting it, it will not be necessary to dwell upon them, since the pulmonary and cutaneous perspiration were estimated together by these observers. The first attempt to estimate separately the vapor exhaled by the skin from that by the lungs was made by Lavoisier[2] and Seguin in 1790, the experiments consisting in enclosing Seguin in a bag of gummed taffeta which was tied above the head, an aperture in the coat when fixed around the mouth by a mixture of turpentine and pitch enabling Seguin to inspire fresh air and exhale the breathed air, but only permitting the pulmonary vapor of the latter to escape from the body. By then deducting the amount of the pulmonary vapor as determined by the loss of weight when enclosed in the gum coat from the total quantity of vapor exhaled as determined by the loss of weight when not so enclosed, the amount of the cutaneous vapor was at last experimentally determined, and was found to be nearly 2 kilos. (2 pounds) which does not differ very considerably from the later results obtained by Krause[3] and Valentin.[4]

The amounts of perspiration exhaled by the skin, as shown by Lavoisier and Seguin and subsequent observers, vary very considerably, however, depending upon the quantity and temperature of the liquid food, the relative dryness or moisture and temperature of the atmosphere, the amount of exercise taken, and the activity of the lungs and kidneys, with which the skin acts vicariously. The skin, however, not only supplements the action of the lungs as

[1] Sanctorii Sanctorii, De Statica Medecina aphorismorum. Lugduni Batavorum, MDCCIII.

[2] Mem. de l'Acad. des Sciences, p. 609. Paris, 1797.

[3] Wagner, Physiology, Band ii., s. 319.

[4] Physiology, Band i., s. 174. Braunschweig, 1844.

regards the exhalation of watery vapor and carbon dioxide, but that of the kidneys also, and not only with reference to the water but to the urea eliminated as well. Thus, according to Carpenter,[1] in one experiment the entire quantity of perspiration for the whole body being in one hour 3,320 grains, 6½ grains of urea, containing 3.03 N, were obtained. It is not likely, however, that the excretion of urea would have continued during the whole twenty-four hours at such a rate. It should be mentioned in this connection also, according to Funke,[2] that through the desquamation of the epidermic scales about 0.7 gramme (11 grains) of nitrogen are also daily eliminated by the skin. According to recent researches the amount of urea excreted in the sweat is also much increased by muscular work.[3]

That the sweat, however, contains other substances than those already mentioned is rendered very probable from the fact that death soon ensues when the perspiration is suppressed, as, for example, when the skin is varnished in animals[4] and also in human beings, as in the celebrated case of the child, who, being covered with gold-leaf to personate an angel at the coronation of Leo X., died a few hours afterward.[5] While death in such cases is no doubt partly due to the imperfect arterialization of the blood and the rapid fall of temperature, the varnish favoring the loss of heat in producing a cutaneous hyperæmia similar to that induced through paralysis of the vasomotor nerves, symptoms like that of uræmic poisoning, tremors, tetanic cramps, movements of rotation, increased reflex excitability, present as well, lead one to suppose that urea and other poisonous substances not yet isolated are retained in the system which are usually carried away in the sweat. That such is the case is shown by the fact that if human sweat be injected into the blood of the rabbit[6] the pulse of the latter may be increased from 192 beats per minute to 326, the respiration from 82 to 105, and the temperature raised from 37.2° to 40° C. (99° to 104° F.). Even if it be admitted that the exact cause of death is not yet positively determined there can be no doubt that imperfect action of the sweat glands must be a source of disease, various matters then accumulating in the system which would otherwise be eliminated. Indeed, too much stress cannot be laid upon the importance of keeping the skin clean—of the free use of water. Especially is such the case in tropical climates where the true secret of maintaining one's health lies in attending to the condition of the skin, and where febrile diseases are more successfully treated by active diaphoresis than in any other way. The great importance of daily baths in the maintenance of health cannot be exaggerated, and ap-

[1] Physiology, p. 491. [2] Moleschott Unters., 1858, Band iv., s. 56.

[3] Argutinsky, Pfluger's Archiv, Band xxxxvi., 1890, s. 552.

[4] Fourcauet, Comptes rendus, Tome vi., p. 369. Paris, 1838. Ibid., 1843, Tome xvi., p. 139. Valentin, Archiv f. Physiologie Heilkunde, 1858, Band ii., s. 433. Bernard, Liquides de l'Organisme, Tome ii., p. 177. Paris, 1859.

[5] Laschkewitsch, Du Bois Reymond's Arch., 1868, s. 61.

[6] Rohrig, Jahrb. für Balneologie, 1873, Band i., s. 1.

parently was more appreciated by the ancients than the moderns, as the ruins of the magnificent baths of Caracalla and Diocletian, at Rome, still to this day testify. Noble institutions they were; the baths or thermæ fed by stupendous aqueducts stretching for miles across the Campagna, their perpetual streams of hot and cold water flowing through mouths of solid silver into capacious basins, accommodating at one time thousands of bathers, and where for the eighth of an English penny the meanest Roman of them all could enjoy the luxury that might have well excited the envy of the kings of Asia.[1]

The secretion of sweat, like other secretions, is influenced by the nervous system, the sweat center or centers, being situated, according to Luchsinger,[2] in the anterior horns of the gray matter of the spinal cord and medulla. From these centers nerve fibers arise, which, passing down the cord, emerge principally with the anterior roots of the third, fourth, and fifth cervical nerves to pass with the brachial plexus to the skin of the upper extremity, and with the anterior roots of the lumbar nerves to supply the lower extremity. The sweat centers may be stimulated directly and reflexly. It is in the latter manner that the sweat centers are excited by muscular exercise, dyspnœa, fear, heat, various substances such as pilocarpin, nicotin, muscarin, and inhibited by cold and atropin.

While the sweat nerves emerge from the spinal cord and run in company with the vasomotor nerves, the secretion of sweat is independent of vasomotor influence except in so far as the blood supplies in the long run the materials for the elaboration of the secretion. This is shown by the fact that stimulation of the sciatic nerve in the cat causes secretion of sweat in the soles of the feet after ligation of the aorta or even after amputation of the limb.[3] It is also a matter of daily observation that, although a person may be pale from terror or nausea, sweating may be profuse, and on the other hand, though the skin may be flushed with fever, sweating is absent. That the sweat nerves are true secretory nerves is still further shown by recent histological researches,[4] their terminal fibers having been followed directly to the secretory cells of the sweat glands.

The manner in which the skin regulates the temperature of the body through the radiation, conduction, etc., of the heat produced within it having already been sufficiently considered, it will not be necessary to treat further of the function of the skin in this respect. While there can be no doubt that absorption in the lower animals and in many of the higher is to a considerable extent carried on by the skin, frogs, lizards, etc., rapidly gaining in weight when immersed in water, some difference of opinion still prevails among physiologists as to what extent the skin in man normally

[1] Gibbon, Decline and Fall of the Roman Empire, Vol. v., p. 237. London, 1807.
[2] Pflüger's Archiv, Band xiii., s. 212; Band xiv., s. 545; Band xv., s. 482; Band xvi., s. 538.
[3] Goltz, Pflüger's Archiv, Band xi., 1875, s. 71. Langley, Journal of Physiology. Vol. xii., 1891, p. 347. [4] Arnstein, Anatomische Anzeiger, Band x., 1895.

acts as an absorbing surface. It may not appear superfluous, therefore, if attention be called to those instances or conditions in which absorption does take place in man by the skin. It is well known, as already mentioned, in speaking of the cause of thirst, that in the case of the shipwrecked sailor the thirst was very much, if not entirely, temporarily relieved by the immersion of the body in the sea, or by wearing clothes wet with the same.[1] In certain cases also, where the introduction of solid or liquid food by the mouth had become impracticable, immersion of the patient in a bath of tepid milk morning and evening not only relieved the thirst, but for some time maintained life, the weight gained being unaccounted for by the enemata also given.[2] It has also been shown that not only does the body gain in weight after immersion in a bath through the absorption of the liquid, but that the skin will also absorb certain salts when dissolved in the same. That the skin is permeable by gas is also well known, it having been shown by Bichat that if a limb be immersed in a putrid gas the latter will be absorbed by the skin, and by Aubert that the skin absorbs about the $\frac{1}{180}$ of the oxygen absorbed by the lungs. Admitting, then, that under certain circumstances the skin undoubtedly can absorb, it still remains undetermined to what extent, under normal conditions, it does absorb. Covered, as the skin usually is in man, almost entirely with more or less clothing, it is difficult to comprehend how or what the skin under such circumstances can absorb, the gain in weight of the body through absorption of the watery vapor of the atmosphere sometimes instanced[3] being due to the absorption of the vapor by the lungs rather than by the skin. We have further seen that through the presence of the sebaceous matter the skin is rendered repellant of water, which thereby renders it very insusceptible to the taking up of foreign substances. Indeed, it is very questionable whether such are ever introduced into the system unless the epidermis be disintegrated, the view sometimes advanced[4] that substances are absorbed by the sweat ducts being very improbable, since the latter are already filled with sweat, and the movement of the sweat, being from below upward, would tend to wash away foreign substances rather than favor their absorption. It would appear, therefore, as we pass from the lower to the higher animals, that the skin loses its significance as an absorbing surface, becoming essentially protective and excretory in function. Nevertheless, though the absorbing power of the skin in the economy of the higher animals may have been superseded by that of the lungs and alimentary canal, under certain conditions it may even in them act

[1] Madden, Experimental Enquiry into the Physiology of Cutaneous Absorption, p. 64. Edinb., 1838.

[2] Currie, Medical Reports, Vol. i., pp. 308–326. Watson, Chemical Essays, Vol. iii., p. 100.

[3] Lining, Phil. Trans., 1743, p. 496. Klapp, Inaugural Essay on Cuticular Absorption, p. 30. Philadelphia, 1805.

[4] Auspitz, Wiener med. Jahrb., 1871. Neumann, Wiener med. Wochenschrift, 1871.

vicariously with the same, as no doubt it does, as regards the excretion of water by the kidneys as well as the lungs.

Sense of Touch or Locality.

The skin acts not only as a general sensory surface through the impressions made upon the epidermis being transmitted thence to the more deeply situated cutaneous nerves, but through its Tactile, Pacinian, and Krause corpuscles, it is endowed with a special modification of sensibility—the tactile sensibility, or the sense of touch, by means of which we not only feel but appreciate to a certain extent the form, size, character or surface, weight, and temperature of objects. While the skin as a whole, therefore, is endowed with a general sensibility more or less acute in different parts of the body, its tactile sensibility, however, is restricted to certain portions of it, and most delicate in those situations where the corpuscles are most abundant. Thus, if the blunt but fine ends of a pair of dividers provided with a graduated bar, or æsthesiometer, be applied to the tip of the tongue—the individual being blindfolded—the two ends of the dividers, though only separated by so much as the $\frac{1}{24}$ of an inch, will be appreciated as two distinct objects. If, however, the dividers be approximated until they are separated by less than that distance, the two impressions, a moment previous distinctly appreciated as such, now fade into one, as if but a single object was touching the tongue. Experimenting in this manner, it was first shown by Weber,[1] and afterward by Valetin,[2] that the sense of touch varies very much in different parts of the body, being most acute at the tip of the tongue and ends of the fingers; least so in the back, as shown as follows:

TACTILE SENSIBILITY.[3]

Parts of surfaces.	Both points of dividers felt when separated by these distances.
Tip of tongue	0.50 of a line.
Palmar surface of third phalanx of fingers	1.00 " "
" " " second " " "	2.00 " "
Dorsal " " third " " "	3.00 " "
Middle of dorsum of tongue	4.00 " "
End of the great toe	5.00 " "
Center of hard palate	6.00 " "
Dorsal surface of first phalanx of fingers	7.00 " "
" quarter of heads of metacarpal bones	8.00 " "
Back of the heel	10.00 " "
Dorsum of the hand	14.00 " "
" " foot	18.00 " "
Sternum	20.00 " "
Five upper dorsal vertebræ	24.00 " "
Middle of " "	30.00 " "

When points of dividers are brought closer than these distances they are felt as one.

[1] Wagner, Physiologie, Band iii., Zweite Abth., s. 524.
[2] Physiologie, Band ii., s. 558.
[3] Carpenter, article Touch, Cyclopædia of Anat. and Phys., Vol. iv., Part 2d, p. 1169.

The sense of touch, like the other senses, can be very much improved by attention and practice. Thus, it is said [1] that the female silk throwsters of Bengal can distinguish twenty different degrees of fineness in the unwound cocoons by the touch alone, and that the Indian muslin weaver makes the finest cambric with a loom of such simple construction that, if worked by the hands of a European, would turn out but little better than canvas. It is also a well-known fact that those persons who are employed in mints, etc., in the daily habit of handling coins, detect at once, and with certainty, a light piece. As might be expected, the sense of touch is very much developed in those who have lost the sense of sight, or who have been blind. One of the most remarkable of such cases is that of Giovanni Gonelli, who, at twenty years of age lost his sight, but who, nevertheless, after a lapse of ten years, developed a great talent as a sculptor, modelling such an excellent statue out of clay of Cosmo de Medici from feeling one of marble that the Grand Duke of Tuscany sent him to Rome to make a statue of Pope Urban VIII., which was a very successful one, the likeness being said to be excellent. Stranger still, even a good knowledge of botany and conchology has been acquired through the sense of touch by persons who have been born blind, or who had lost their sight early in life. It is well known, also, as in the case of Baczko,[2] that the blind can learn to distinguish the colors of fabrics by the sense of touch. It is related that Sanderson, the blind professor of mathematics at Cambridge, could not only distinguish different medals, but could detect imitations of them often better than professed connoisseurs, while his appreciation of variations of temperature, it may be mentioned also,[3] was so acute that he could tell, through slight modifications in the temperature of the air, when very slight clouds were passing over the sun's disk. It is a familiar fact, also, that the blind learn to read with great facility by passing their fingers over raised letters of about the size of those of a folio Bible. Terrible a calamity as the loss of sight is, it should not be forgotten, as the above examples teach us, what a delicate sense in that of touch we possess if cultivated, and that sources of pleasure and recreation through its development may be offered to those who are born blind, or who have lost their sight later in life.

The sense of touch next to that of sight is the most important means by which we gain our knowledge of the external world. Indeed our appreciation of the form and qualities of external objects is based almost entirely upon the association of tactile and visual sensations together with those due to the so-called muscular sense. It may be recalled in this connection that the center for touch is usually regarded as being located in the hippocampal region of the cortex.

[1] Carpenter, op. cit., p. 1177.
[2] Rudolphi, Physiologie, Band ii., s. 85.
[3] Dunglison, Physiology, Vol. i., p. 697. Phila., 1856.

Sense of Pressure or Weight.

The sense of pressure or of weight is the sense by means of which we appreciate the amount of pressure that is exerted upon the skin. The part of the skin endowed with this sense appears to be especially modified, being characterized by the presence of the so-called "pressure spots" or "pressure points" (Fig. 414) for the reception of stimuli.

FIG. 414.

Pressure-spots. *a*. Middle of the sole of the foot. *b*. Skin of zygoma. *c*. Skin of the back. (LANDOIS.)

The minimal distance at which two pressure spots, when stimulated, give rise to distinct sensations, varies in different parts of the skin, being in the palm of the hand, for example, from 0.1 to 0.5 mm., on the back from 4 to 6 mm. The smallest perceptible pressure varies, also, according to the locality. Thus a pressure exerted by 0.002 grms. will be appreciated if the weight be applied to the forehead, temple, back of the hand, and forearm, 0.005 to 0.015 grms. are felt by the fingers, 0.04 to 0.5 grms. by the chin, abdomen, and nose, 1 gr. by the finger nail.[1] Variations are also manifested by the skin in the power of discriminating differences of pressure. Thus, according to Eulenberg, the forehead, lips, and temples appreciate the difference between 200 and 205 grms. or $\frac{1}{40}$ and 300 and 310 grms. or $\frac{1}{30}$, the head, fingers, and forearm, the difference between 200 and 220 grms. or $\frac{1}{10}$ and 200 and 210 grs. or $\frac{1}{20}$.

The smallest additional weight appreciated as a difference when added to 1 grm. resting upon the skin is according to Dohrn in the case of the first phalanx of the finger 0.02 grm., third phalanx 0.49 grm., back of the foot 0.5 grm., palm 1.01 grm., back 3.8 grms.[2] It is a well-known fact that pressure due to a uniform compression such as is exerted upon a finger dipped into mercury, for example, is not felt as such but only at the surface of the level of the fluid. If the weights made use of in experimenting upon the sense of pressure are comparatively heavy ones and the pressure has been exerted for some time the sensation produced persists even after removal of the weight as the so-called "after-pressure." Even in the case of light weights being used an interval of time amounting to at least from $\frac{1}{500}$ to $\frac{1}{600}$ of a second must elapse in order to appreciate the difference, the sensations becoming fused when the intervals of application are shorter. Thus it has been shown that when the fingers are pressed against a toothed wheel, the sensation experienced was a smooth one when the teeth touched the skin at the intervals just mentioned, whereas each tooth caused a distinct sensation when the wheel was rotated more slowly. It is also well known that vibrations of strings cease to be distin-

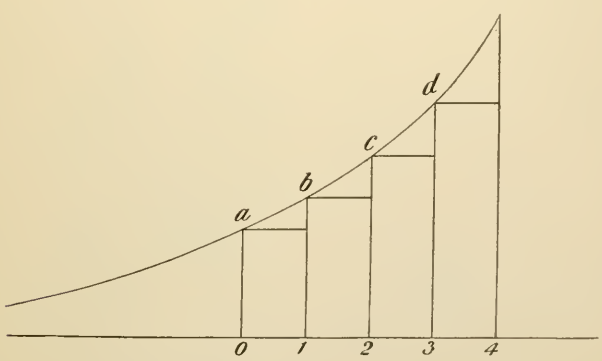
[1] Anbert u. Kammler, Moleschott Untersuchungen, Band v., 1859, s. 145.
[2] Landois, op. cit., p. 1053.

guished as such when the rate of vibration exceeds that of 1,600 per second.

It has been established by the researches of Weber[1] and Fechner[2] that in the case of the sense of pressure, and as we shall see presently, in that of all kinds of sensation there is a strength of stimulus varying for each sense, the so-called "liminal intensity," which is just powerful enough to awaken sensation. On the other hand, there is also a strength of stimulus, the so-called "maximum of excitation," beyond which no increase of sensation will be felt by any further increase of stimulus. There is, therefore, for each sense a "range of sensibility," the range extending between these two limits. It has also been shown that as the strength of the stimulus increases, so also does the sensation, but that the latter increase equally when the amount of stimulus necessary to cause a perceptible increase of sensation bears the same ratio to the amount of stimulus already applied. Thus, for example, the eyes being bandaged and the hand extended and supported, if weights such as 10, 100, 1000 grammes be successively placed in the hand, it will be found that one-third of the original weight, 3.3 or 33.3 grs., etc., must be always added, according to whichever weight be used in order to appreciate any increase in weight. The fractional increment of the original weight necessary for the discrimination, one-third in the case of weight, is called "the constant proportion." The "liminal intensity" and the "constant proportion" being known, the data are given by which the general relation of the sensation to the stimulus can be shown graphically.

Suppose, for example, that the sensation under consideration be one of pressure, let the horizontal line $o\,x$, or the abscissa (Fig. 415), be divided into equal parts, 1, 2, 3, 4, to represent equal in-

FIG. 415.



Graphic illustration of reaction of sensation to stimuli.

crements of sensation, the zero corresponding to the minimum of sensation, the vertical lines, or the ordinate $0a$, $1b$, $2c$, $3d$, $4e$, the

[1] Vorlesungen, Band i., Leipzig, s. 133.
[2] Elemente Der Psychophysik, Band ii., Leipzig, s. 377.

stimuli, $0a$ corresponding to the minimum stimulus, say one-fiftieth of a gramme, each ordinate being equal to the preceding one plus a third of the same, according to the determination of the constant proportional in the case of weight; it is evident that the difference of length between the line $0a$ and the lines $1b$, $2c$, $3d$, $4e$, indicates the weights that must be used in order that the successive sensations should be equal.

As the logarithms of the stimuli increase, however equally, as well as the sensations, when the stimulus is increased in such constant proportion it follows that the sensation is not proportional to the stimulus but to the logarithm of the stimulus.[1] In other words, if the sensations are as 1, 2, 3, the stimuli are as 10, 100, 1000; 1, 2, 3, being the logarithms respectively of 1, 10, 1000.[2] This so-called Fechner's psycho-physical law of sensation only holds good, however, when the stimuli used are of medium strength, since as we have seen when very light or very heavy weights are used, the increment of pressure necessary for sensation is not a constant proportion of the original stimulus.

Muscular Sense.

By means of the muscular sense we learn the position of the different parts of our bodies, become aware of the density, elasticity, immobility due to the resistance offered by external objects, realize the effort we make when exerting a pressure upon the same, and appreciate the condition of our muscles and the extent of their contraction. By the muscular sense we learn far more accurately the weight of an object when supported by the hand by muscular effort than when the object simply presses upon the hand, the latter being supported and extended, we not only feel in the first case the pressure of the object, but are also conscious of the exertion required to lift and support the weight. It is well known that an individual affected with locomotor ataxia, while retaining the sensations of touch, temperature, pain, is unable to coördinate his muscles, and on the other hand, that in certain kinds of nervous diseases, while sensation may be impaired or abolished, the power of muscular coördination may be retained. A frog can also coördinate his muscles after entire removal of the skin, and, therefore, in the absence of all cutaneous sensation. It has also been shown by Weber,[3] as a general rule, that while differences in weight are appreciated most acutely by those parts of the skin which are most sensitive to the impressions of touch, as that of the fingers, for example, that, while by the sense of pressure alone a difference in weight of not less than one-eighth can only be determined, by making a muscular

[1] W. Wundt, Grundzüge Der Physiologischen Psychologie, Band i., 1880, s. 358.

[2] A logarithm of a number is the exponent of the power to which it is necessary to raise a fixed number to produce the given number. Suppose the fixed number to be 10, the given number 100 or 1000, then 2 and 3 will be the logarithms of 100 and 1000 respectively, since $10^2 = 100$, $10^3 = 1000$.

[3] Wagner, Physiology, Band iii., Zweite Abth., s. 543.

effort, as in lifting, a difference of one-sixteenth can be accurately appreciated.

Such considerations as those just mentioned have led many physiologists to regard the muscular sense as due to impulses derived from the muscles, tendons, and joints as well as from the skin. On the other hand, the ataxic symptoms present in certain nervous diseases, where sensation is impaired and often referred to as a proof of the existence of a special muscular sense normally, are perfectly well accounted for by other physiologists by the loss of general sensibility. Since the impression made by the foreign body, whether it be the ground we tread upon or the child we hold in our arms, not being transmitted to the encephalon, in such cases it will not be reflected consciously or otherwise to the appropriate muscles whose action enables us to stand securely or grasp firmly, hence our inability to walk upon the ground or hold a child in our arms unless we look at the one or the other, the essential reflex action being then effected by the eye and optic nerve instead of the skin and cutaneous nerves.

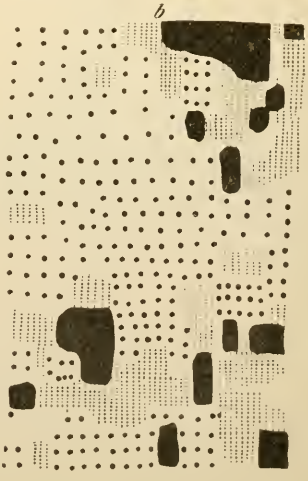
The "constant proportion" for the muscular sense is usually regarded as being $\frac{6}{100}$.

Sense of Temperature.

By means of the sense of temperature we appreciate the changes in the heat of the skin, the latter being specially modified, presenting the so-called "temperature spots" for the reception of impulses from hot and cold bodies. The cold (*a*) and hot (*b*) spots (Figs. 416, 417) can be mapped out by touching the skin with a

FIG. 416.

FIG. 417.



Cold- and hot-spots from the same part of the anterior surface of the forearm. *a*. Cold-spots. *b*. hot-spots. The dark parts are the more sensitive, the hatched the medium, the dotted the feeble, and the vacant spaces the non-sensitive.

blunt-pointed metal rod previously warmed or cooled. The cold points appear to be more numerous than the hot ones. The minimal distance at which the cold spots can be appreciated is, in the case of the forehead, 0.8 mm., and in that of the hot spots 4 to 5 mm. The skin is more sensitive to cold than to heat, that of the left hand greater in this respect than that of the right. The skin varies very much also in regard to its susceptibility to changes in temperature, that of the palm, for example, appreciating a difference of 0.2° C., of the breast 0.4° C., leg 0.6° C., back 0.9° C. In the case of the sense of temperature, as in that of pressure, the "constant proportion" is one-third of the original stimulus.

It is worthy of mention in this connection that the mucous membrane of the alimentary canal, from the œsophagus to the rectum inclusive, is not endowed with the power of discriminating between differences of temperature. An enema of water cooled down is only appreciated as being cold when the water passes over the skin of the arms.

Sense of Pain.

It has already been mentioned that difference of opinion still prevails as to whether the sense of pain is due to impulses transmitted by special nerves, or to the impulses usually giving rise to pressure, heat and cold being simply exaggerated. Those who hold the former view, argue that the skin is endowed, like other tissues, with general sensibility and when the afferent nerves ministering to the latter are so excited as to affect consciousness, pain results.

CHAPTER XXXVII.

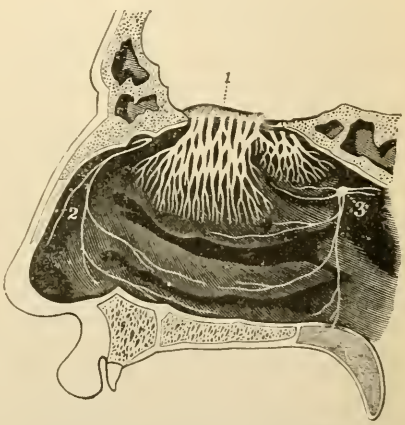
THE NOSE AND OLFACTION. THE TONGUE AND GUSTATION.

Just as we have seen that the skin, in addition to its other functions, acts as a general sensory organ, so we shall soon learn through the study of Development, that parts of it being especially modified become very susceptible to certain external impressions, and that such modifications, together with corresponding ones developed in the terminal nerves supplying the parts, constitute special sensory organs, such as the nose, tongue, eye, and ear, and inasmuch as, of such organs, the nose is the most simple in structure, we will begin the consideration of the special senses with the study of Olfaction.

Olfaction.

The nose, the special organ of the sense of smell, is regarded anatomically as being limited to the pyramidal eminence of the face, extending from the forehead to the upper lip; physiologically, however, the nose—that is, the organ of olfaction—includes not only the parts just mentioned, consisting of the septum, cartilages, etc., but of the nasal cavities as well; the mucous membranes lining the latter being endowed not only with general sensibility, as we have seen, but with the special sense of olfaction, its upper half being supplied (Fig. 418) by the olfactory nerve, the special nerve of the sense of smell. The skin of the nose, thin above but thick below, as elsewhere, is furnished with sudoriferous and sebaceous glands and hairs; the hairs are usually small except within the margin of the nostrils, in the latter position, however, they are well developed from all sides, and to a certain extent act like a fine sieve in keeping out dust, etc. The nasal cavities communicating with the exterior, in front, by the anterior nares, and with the pharynx, behind, by the posterior nares, are lined with a mucous membrane

Fig. 418.



Distribution of nerves in the nasal passages. 1. Olfactory ganglia, with its nerves. 2. Nasal branch of fifth pair. 3. Spheno-palatine ganglion. (Dalton.)

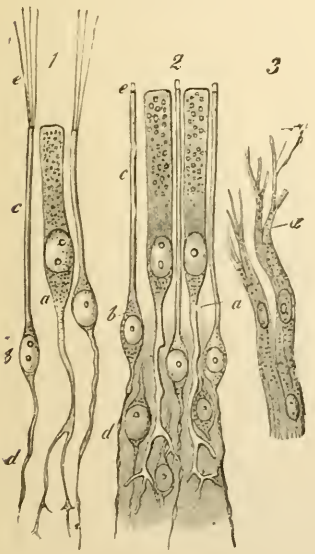
closely applied to the adjacent periosteum and perichondrium, which becomes, at the nostrils, continuous with the skin, at the posterior nares, with the mucous membrane of the pharynx, and at the lachrymo-nasal duct and lachrymal canals with the conjunctiva. The nasal mucous membrane differs very much in its character according to its situation. Thus on the part lining the so-called "olfactory region," or that covering the upper part of the septum, the superior and part of the middle turbinated bones is thick, highly vascular, and covered with a columnar epithelium amidst the cells of which occur peculiar rod-like cells. The latter we shall see presently are the olfactory cells in which the fibers of the olfactory nerve terminate or rather arise just as we have seen the axis-cylinders in the anterior roots arise from cells in the cord. On the other hand, the remaining portion of the nasal mucous membrane, the so-called Schneiderian or pituitary membrane, or the part lining the "respiratory region," that is covering the lower part of the septum, part of the middle and inferior turbinated bones, is covered with a columnar ciliated epithelium (except within the nostrils where it is squamous), the current due to the cilia being directed towards the pharynx. The nasal mucous membrane is also provided with glands whose secretion keeps the surface moist, a condition essential to the accurate perception of odoriferous impressions. The glands of the true olfactory membrane, the so-called Bowman glands, are tubular or mixed glands.

The special nerves of the sense of smell or the true olfactory nerves are given off as fifteen to eighteen filaments from the olfactory bulb to the olfactory region. The olfactory tract, of which the ganglionic bulb is the expansion, is usually described as the olfactory nerve, but improperly, since, as development shows, the olfactory tracts are outgrowths of the cerebral hemispheres, their morphological significance masked in man by the excessive development of the former. The olfactory tracts are two cords or bands, soft and friable, consisting of both white and gray nervous matter, which, passing forward and inward on the under surface of the anterior lobe of the cerebrum to the ethmoid bone, expand at the side of the crusta galli into the olfactory bulbs, from which are given off, as just mentioned, the true olfactory nerves, which, passing through the cribriform foramina of the ethmoid bone, are distributed to the inner and outer walls of the upper parts of the nasal cavities. Each olfactory tract arises apparently by three roots, from the inferior and internal surface of the anterior lobe of the cerebrum in front of the anterior perforated space, the external and internal roots being composed of white matter, the middle of gray, the large proportion of the gray substance, one-third, entering into the composition of the olfactory tract, confirming what has just been said as to the true nature of the latter. While the anterior root can be traced into the middle lobe and the middle and internal roots into the anterior lobe, considerable obscurity still

prevails as to the deep origin of all three roots. It would appear, however, that the long or external root originates in the island of Reil, the thalamus opticus and the nucleus in the temporo-sphenoidal lobe in front of the hippocampus, the middle or gray root in the gray substance of the anterior perforated space, the inner root in the gyrus fornicatus. The true olfactory nerves, or the filaments given off from the olfactory bulb, as they descend from the cribriform plate ramify, and, uniting in a plexiform manner, spread out laterally in brush-like and flattened tufts (Fig. 418). In their minute structure, the olfactory differ from the ordinary cerebral and spinal nerves in being pale and finely granular, in not possessing a substance of Schwann, in adhering to one another, and in presenting oval corpuscles.

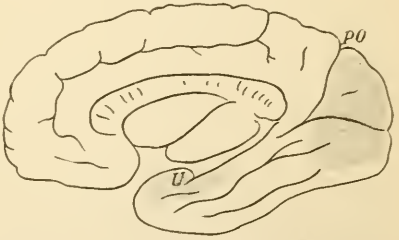
Their manner of termination is also peculiar, each olfactory fiber appearing to pass into the spindle-shaped bodies (*b*) interspersed between and among the epithelial cells (*a*) of the olfactory membrane (Fig. 419). These olfactory cells, so-called on account of their

Fig. 419.



Cells and terminal nerve-fibers of the olfactory region, highly magnified. 1. From the frog. 2. From man. *a*. Epithelial cell, extending deeply into a ramified process. *b*. Olfactory cells. *c*. Their peripheral rods. *e*. Their extremities, seen in 1 to be prolonged into fine hairs. *d*. Their central filaments. 3. Olfactory nerve-fibers from the dog. *a*. The division into fine fibrillæ. (Frey after Schultze.)

Fig. 420.



Inner aspect of the right hemisphere. *po*. position of the visual center in the occipital lobe *U* of the olfactory center in the uncinate gyrus. (Gowers.)

supposed function, present a very characteristic appearance, the central nucleated portion passing on the one hand internally into a beaded varicose-like thread (*d*) apparently continuous with the terminal olfactory fibril, and, on the other, externally into a rod-like structure (*c*), which in the frog is prolonged into fine hairs. That the olfactory cells, nerves, bulbs, and tracts, constitute the essential structures, by which external impressions are transmitted to the subiculum cornu of the hippocampal convolution,[1] in which the sense of smell is supposed to be localized (Fig. 420), is proved by the harmonious results of experi-

[1] Obersteiner, op. cit., s. 360. Edinger, op. cit., s. 201. Rauber, op. cit., s. 674.

ments performed upon animals, of pathological cases observed in man, and of the facts of comparative anatomy. Thus, among the numerous experiments in which the olfactory tracts were divided, and the loss of the sense of smell noticed, may be mentioned those performed upon hunting dogs by Vulpian[1] and Philipaux, in which cases the animals, although deprived of food for thirty-six hours after complete recovery from the effects of the operation failed to find the cooked meat concealed in the corner of the laboratory. That destruction of the olfactory nerves, bulbs, or tracts in man due to disease or injury involves the impairment or loss of the sense of smell is well known to pathologists, a number of such cases having been observed by Schneider, Rolpinck, Eschricht, Fahner, Valentin, Rosenmuller, Ceneti, Pressat,[2] Hare,[3] Notta,[4] Ogle,[5] Flint.[6] That the olfactory bulbs and nerves are the essential organs of the special sense of smell is still further shown by the fact that they are usually best developed in animals in which the sense of smell is most acute, being better developed, for example, in the mammalia than in the remaining vertebrates, while of the former class it is among those orders, as in the carnivora, in which the sense of smell is very acute, that the olfactory region is most developed, in the dog, for example, in which the sense of smell, as well known, is very remarkable. The olfactory nerves, though readily impressed by odorous emanations, are but little affected by ordinary, while the olfactory tracts appear entirely insensible to the latter.[7] That the appreciation of odors or olfaction is due to the material emanations given off by odoriferous substances being carried by the inspired air to the terminal filaments of the olfactory nerves, the olfactory cells, is shown by the manner in which one sniffs the air in order to perceive an odor, and from the fact that if the air does not pass through the nostrils, as in occlusion of the posterior nares or in division of the trachea, the sense of smell is abolished. In every case where odorous emanations are perceived, the latter must impinge upon the olfactory membrane, come in contact, excite the peripheral ends of the olfactory nerves.

According to Passy[8] as small a quantity of musk as the 0.000005 gramme in one liter of air can be appreciated, the amount of oil of peppermint that can be recognized being still smaller, 0.00000005 gramme, while according to Fisher and Penzoldt[9] $\frac{1}{460000000}$ of a milligrame of mercaptan in 1 c.cm. of air can be

[1] Leçons sur la physiologie générale et comparée du systeme nerveux, p. 882, note. Paris, 1866.

[2] Cited by Longet, Anat. et Phys. du systeme nerveux, Tome ii., p. 38. Paris, 1842.

[3] A View of the Structure, etc., of the Stomach and Alimentary Organs, p. 145. London, 1821.

[4] Archives générales de médicine, p. 385. Paris, Avril, 1870.

[5] Medico-Chirur. Trans., Lond., 2d ser., Vol. xxxvii., p. 263.

[6] Flint, Physiology, 1874, Vol. v., p. 39.

[7] Magendie, Journal de physiologie, Tome iv., p. 169. Paris, 1824.

[8] Comptes Rendus Soc. de Biologie, 1892, p. 84.

[9] Landois, op. cit., p. 1039.

detected. Like the sense of touch, and the other special senses, that of smell may be very much developed by practice; as exemplified in the discrimination of the quality of wine, drugs, etc. It is well known that the boy, James Mitchell, who was deaf, dumb, and blind, made use of his sense of smell like a dog to distinguish persons and objects.

The sense of smell is, however, far more acute in the lower races of mankind than in the higher ones, to whatever extent in the latter it may have been developed by cultivation. Thus it is said that the Mincopies of the Andaman Islands scent the ripeness of the fruits; that the Peruvian Indians distinguish the different races of mankind by scent alone; that Arabs can smell a fire thirty miles off; that the North American Indians pursue by smell their enemies or their game. However the sense of smell may be developed in man, it is far surpassed in acuteness by that of animals. Every sportsman is aware that odors are recognized by hunting dogs, to which he is entirely insensible.

The sense of smell is intimately related to that of taste, so much so, indeed, that if the nose be held, or plugged up, the characteristic taste of certain substances when swallowed, is not appreciated at all, as illustrated in drinking different kinds of wine, it being difficult, usually impossible, to distinguish the same under such circumstances. Further, it has been observed in those cases in which the sense of smell is lost, that of taste is usually lost also.

As a general rule, persons having offensive emanations from the respiratory organs are not aware of such, not appearing to be affected by odors passing from within outward through the nostrils. This is due, not so much to the odor being carried by the air expired through the nostrils instead of by that inspired, as to the fact that one becomes in time accustomed to such odors, and ceases to notice them, however fetid they may be.

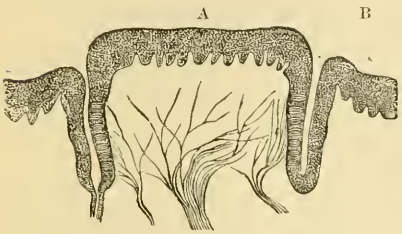
The influence exercised by the nose upon respiration has already been mentioned. We shall see, hereafter, that the nose, also, modifies very much the quality of the voice.

The Tongue and Gustation.

The sense of taste, or gustation, enabling us to appreciate the savor of sapid substances when introduced into the mouth, is due to the susceptibility of the terminal filaments of the chorda tympani and glosso-pharyngeal nerves, of being impressed by contact of the same. The influence of the tongue in mastication and deglutition, the origin, distribution, and general functions of the chorda tympani and glosso-pharyngeal nerves having been considered, it only remains for us now to point out the manner in which gustation is performed through the parts just mentioned. That the tongue is the organ of gustation there can be no doubt. It would appear, however, from experiments such as those performed by

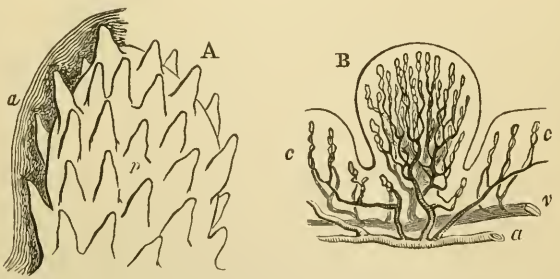
Longet[1] and others, in which different parts of the mucous membrane are touched with a sponge soaked in a sapid solution, that the sense of taste, probably in man at least, is limited to the dorsal surface of the tongue, and from the experiments of Camerer,[2] in which solutions were applied through fine glass tubes, more particularly to the circumvallate and fungiform papillæ, the parts around the latter not appearing to be impressed by sapid substances. The circumvallate papillæ (Fig. 421), so called on account of each papilla being surrounded by a trench or fossa, from seven to twelve in number, are disposed in two rows (in the form of a V, the open angle of the latter being directed forwards), on the back part of the tongue. Each papilla is covered by numerous small secondary papillæ, the latter, however, being concealed by the thick and stratified epithelium. The fungiform papillæ, more numerous than the circumvallate, and readily distinguished during life by their deep red color, while found in the middle and forepart of the dorsum of the tongue, are most numerous and closely set together at the apex and near the borders. Each fungiform papilla, while narrow at its attachment (Fig. 422), at its free extremity is blunt and rounded, and, like

Fig. 421.



Vertical section of circumvallate papilla, from the calf. 35 diameters. A. The papilla. B. The surrounding wall. The figure shows the nerves of the papilla spreading toward the surface, and toward the taste-buds which are imbedded in the epithelium at the sides; in the sulcus on the left the duct of a gland is seen to open. (Engelmann.)

Fig. 422.



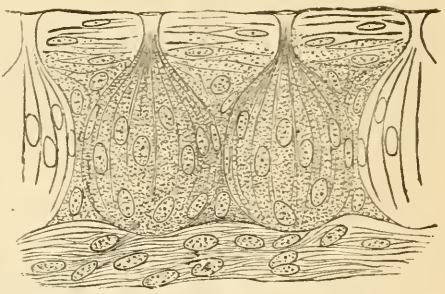
Surface and sectional view of a fungiform papilla. A. The surface of a fungiform papilla partially denuded of the epithelium. (35 diameters.) *p.* Secondary papillæ. *a.* Epithelium. B. Section of a fungiform papilla with the blood vessels injected. *a.* Artery. *v.* Vein. *c.* Capillary loops of simple papillæ in the neighborhood, covered by the epithelium. (From Kölliker, after Todd and Bowman.)

the circumvallate papillæ, is covered with secondary papillæ and epithelium. Imbedded in the epithelium, and more particularly in that of the circumvallate papillæ, are found ovoidal flask-shaped

[1] Physiologie, Tome iii., p. 52. Paris, 1873.
[2] Zeitschrift für Biologie, 1870, Band vi., s. 440.

bodies (Fig. 423), having a length of the $\frac{1}{14}$ of a mm. ($\frac{1}{350}$ of an inch), and a diameter of the $\frac{1}{64}$ of a mm. ($\frac{1}{1600}$ of an inch), consisting apparently of modified epithelial cells, which, with good reason, are supposed to be the special organs of the sense of taste.[1] Each ovoid body, surrounded by flattened epithelial cells, consists of a cortical and a central part. The former is composed of long, flattened, tapering cells, disposed edge to edge, and coming to a point at the taste-pore, the latter of spindle-shaped taste cells. The latter resemble very closely the olfactory cells; the distal end of the cell projecting from the orifice of the taste-bud, and the central beaded, varicose end being continuous with the terminal filament of the gustatory nerve. Such being the disposition of the taste cells, it would appear that the terminal filaments of the gustatory nerves,[2] of which the former are the continuation, are excited by the flow of sapid solutions through the taste-pore into the interior of the taste-bud; the taste cells being especially susceptible to impressions made by substances in solution, whence the impression is transmitted by the chorda tympani and glosso-pharyngeal nerves to the centers of taste, localized in the subiculum cornu of the hippocampus (Fig. 375, U), where they are perceived. That the chorda tympani and the glosso-pharyngeal nerves are the special nerves of the sense of taste, the former more particularly for the anterior two-thirds of the tongue, the latter for the posterior third, can be shown, as already mentioned, both by experiments performed upon animals, and by pathological cases observed in man, division or disease of these nerves involving loss of the sense of taste. The glosso-pharyngeal differs from the chorda tympani, however, in this respect, in that it is a nerve of general sensibility, as well as that of taste, the chorda tympani (gustatory fibers) being a nerve of taste alone, the sensory fibers of the lingual nerve bearing to the chorda tympani the same relation that the sensory fibers of the glosso-pharyngeal bear to its gustatory ones.

Fig. 423.



Two taste-buds from the papilla foliata of the rabbit. (450 diameters.) (Engelmann.)

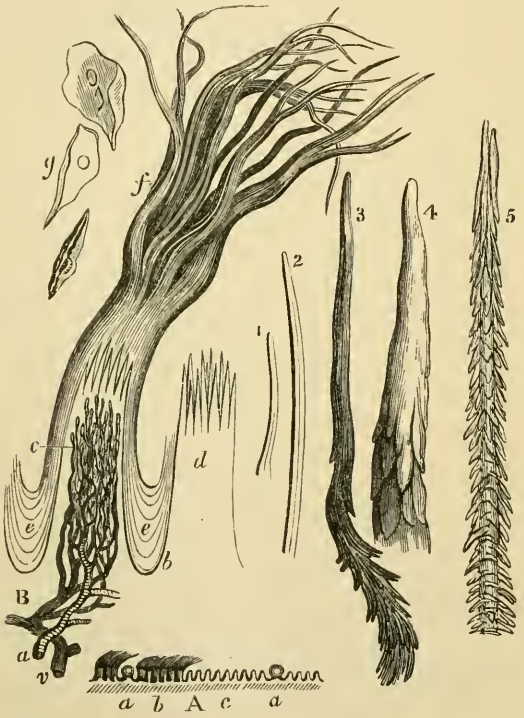
It should be mentioned, however, that according to Gowers[3] any gustatory properties that the glosso-pharyngeal possesses is due to fibers derived from the fifth nerve through the otic ganglion, tympanic plexus, and petrous ganglion.

It is generally admitted that all gustatory sensations are made up of four primary sensations, sweet, bitter, acid, and saline. It is

[1] Rauber, op. cit., s. 694. [2] Edinger op. cit., s. 40. [3] Op. cit., Vol. ii., p. 278.

also regarded as probable that there are distinct nerve fibers for the transmission of impulses to special cortical centers, which when respectively excited, give rise to the above special sensations. However that may be, it has been shown as a matter of fact,[1] that potassium chloride tastes cool and saltish at the anterior part of the tongue, and sweetish at the posterior part; potassium nitrate cool and piquant at the anterior, and bitter and insipid at the posterior end. Certain substances, like mineral acids, ferric sulphate, jalap, and colocynth, while but little appreciated at the anterior part of the tongue, are appreciated very acutely at the posterior portion. On the other hand, meats, milk, and wines, are equally well appreciated at both ends of the tongue.

FIG. 424.



Filiform papillæ. (QUAIN.)

The time which elapses between the application of a sapid substance and the resulting sensation varies with different substances. Thus according to Van Vintschgan[2] saline substances are tasted most quickly within the 0.17 sec., then sweet, acid, and bitter ones; the latter in the case of quinine within 0.258 sec. It is well known that the sense of taste is much aided by that of smell, the two sen-

[1] Lussana, Archives de Physiologie, Tome ii., 1869, p. 208.
[2] Landois, op. cit., p. 1042.

sations together giving rise often to that of flavor. The sense of taste is aided also by that of sight. Thus, for example, if the eyes be bandaged and red and white wine be rapidly tasted alternately it becomes impossible in a short time to distinguish one from the other. The most favorable temperature for taste appears to be between 10° and 35° C. (50° to 95° F.), hot and cold water paralyzing taste at least temporarily. The sense of taste like that of smell is susceptible of great improvement.

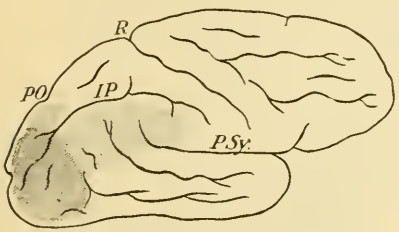
It may be mentioned incidentally that the filiform papillæ, the minute conical eminences densely set over the greater part of the dorsum of the tongue and disposed in lines diverging from the raphe, appear to be tactile in function.

CHAPTER XXXVIII.

THE EYE AND VISION.

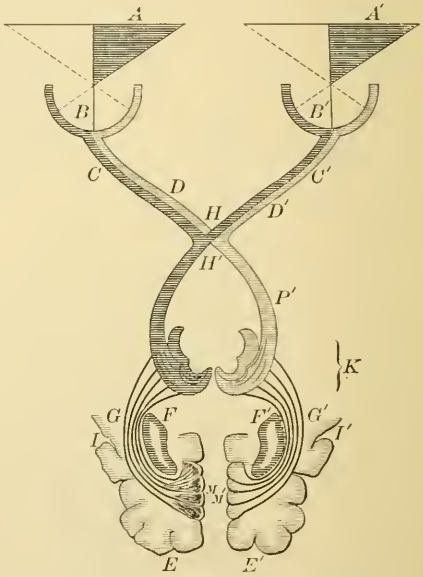
The organ of vision includes the optic nerve, the eye and its appendages. The optic nerves—consisting of medullated fibers but without neurilemma, together with some gray nerve fibers—are usually described as arising from the optic chiasma, or commissure. Regarded, however, as the continuation of the optic tracts, the optic nerves in reality arise, as we have seen, from the optic lobes, thal-

Fig. 425.



Cortical visual centers on the outer surface of the hemisphere. The darker shading indicates the region of the half vision center (the precise limitation of which is not yet known); the lighter shading is that of the supposed higher visual center. (Gowers.)

Fig. 426.



Right homonymous lateral hemianopsia, from lesion of the left visual center of the cortex or left optic tract. *A*. Dark left nasal half field from blind temporal half of retina. *A′*. Dark right temporal half field from blind nasal half of retina. *B*. Left eye. *B′*. Right eye. *C*, *C′*. Left and right optic nerves, composed of the cross bundles of fibers. *D*, *D′*. Left and right crossed bundles. *E*, *E′*. Left and right occipital lobes. *F*, *F′*. Left and right posterior horns. *G*, *G′*. Optic radiation. *H*, *H′*. Optic chiasm. *I*, *I′*. Angular gyrus. *K*. Region of optic thalamus, geniculate body and quadrigeminal bodies, collectively termed primary optic centers. *M*, *M′*. Cuneus. The left cuneus and optic tract are shaded, to show lesion of these parts and the influence of the lesion upon the retina. (Mills.)

ami optici, corpora geniculata, cuneal portions of the occipital lobes, and probably also from the angular gyri. The root fibers (438,000 in number)[1] from these different points of origin, converging, form flattened bands, which, winding obliquely around the under surface of the crura cerebri, pass to the temporal side of one eye and to the nasal side of the other, the decussation of the fibers in the chiasma being therefore incomplete (Fig. 426), at least such is the view held by most neurologists as explaining best the facts of homonymous lateral hemianopsia. Nevertheless, it must be admitted that Kölliker[2] and

[1] Salzer, Wiener Sitzungsberichte, Band 81, 1880, s. 3. [2] Op. cit., s. 563.

other histologists of authority hold that the decussation of the fibers in the chiasma in man is complete. The extent of decussation in animals, which is variable, appears to depend upon the amount of separation of the fields of vision. Thus in man and certain mammals, where the eyes are so placed that they can both be directed to the same object, the fields of vision overlap and there is incomplete decussation. On the other hand, in the lower mammals, such as the mouse and guinea-pig, birds (with the exception perhaps of owls), reptiles, amphibia, and fishes, in which the fields of vision are distinct and do not overlap, there is a total decussation. It should be mentioned, however, that the fibers constituting the anterior portion of the chiasma are not derived from the optic tracts, but simply pass from one eye to the other, while the fibers constituting the posterior part—and sometimes wanting—pass from tract to tract without being connected with the eyes. The optic nerves proper, arising from the anterior and outer border of the chiasma, curved in direction and rounded in form, enclosed in a double fibrous sheath, derived from the dura mater and arachnoid, pass into the orbit through the optic foramina, piercing the sclerotic coat of the eye at its posterior, inferior, and internal portions; the thin, but strong membrane through which the nervous filaments pass into the sclerotic, known as the lamina cribrosa, being partly derived from the sclerotic, and partly from the coverings of the nerve fibers which are lost at this point. At about 5 millimeters ($\frac{1}{5}$ of an inch) behind the globe of the eye, the optic nerve receives the central artery and vein of the retina, which, together with a delicate filament from the ophthalmic ganglion, is thence transmitted within the center of the nerve by a minute canal, lined with fibrous tissue. That the optic nerves are the special nerves of the sense of sight there can be no doubt, since their injury or division always involves impairment or loss of sight. While the optic nerves are the avenues or paths by which the impressions due to the presence of light are transmitted to the cunei and angular gyri, there to become, as we have seen, conscious, intelligent vision, they are, however, absolutely insensible to ordinary impressions. Not only have these nerves been pinched, cut, and cauterized in animals, without the latter evincing any pain, but their insensibility in man has often been observed also, as in surgical operations, for example, in which the nerves have been exposed. That the optic nerves are especially susceptible to the impressions of the rays of light is still further shown from the fact of their excitation, however caused, always giving rise in consciousness to the idea of light—a severe blow on the orbit making one see stars, as often said, the mind having associated so uniformly the excitement of the optic nerve with the presence of light, that in time it becomes impossible to disassociate the two; the excitement of the one invariably suggesting the presence of the other.

The Eyeball.

The eyeball, a spheroidal body, partly imbedded in a cushion of fat, protected by the surrounding bony orbit and the eyelids, moistened by the lachrymal secretion, and moved by various muscles, is composed of several coats, concentrically disposed, and enclosing several refractive media. Were it not for the fact of the cornea being set in the sclerotic, like a crystal into the rim of the face of a watch, the eyeball would present the form of a spheroid. Owing, however, to the cornea constituting one-tenth of the outer circumference of the eye, and to the fact just mentioned, the longest diameter is in the antero-posterior direction, as shown by the mean results obtained by Sappey.[1]

Diameter of Eyeball in Millimeters.

	Ant. post.		Transverse.	Vertical.	Oblique.
Mean of 12 females from 18 to 81 years of age,	23.9	(0.96 inch.)	23.4	23.0	23.8
Mean of 14 males from 20 to 79 years of age,	24.6	(0.98 inch.)	23.9	23.2	24.1

It will be observed, from the above, that all the diameters are less in the female than in the male. It may be appropriately mentioned in this connection, also, that all such measurements should be made as soon as possible after death, within from one to four hours, owing to the eyeball losing so soon its normal form and dimensions.

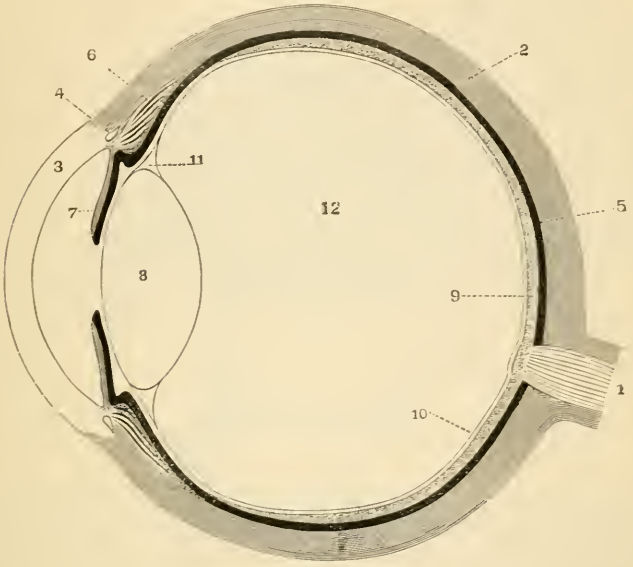
The Sclerotic and Cornea.

The sclerotic (Fig. 427, 2), the outer protective coat of the eyeball, covering the posterior five-sixths of the latter, varying in thickness from 1 to $\frac{1}{2}$ mm. ($\frac{1}{25}$ to the $\frac{1}{50}$ of an inch), is a dense white, opaque tunic, composed of ordinary connective tissue, mixed with small elastic fibers and a few blood vessels, and yielding, on boiling, gelatine. The cornea, the first of the refractive media, constituting the anterior sixth of the outer circumference of the eyeball, and varying in thickness from 1.1 to $\frac{1}{1.2}$ mm. ($\frac{1}{22}$ to the $\frac{1}{32}$ of an inch), is the transparent projecting tunic (Fig. 427, 3) attached to the periphery of the sclerotic, of which, indeed, it may be regarded as the continuation, consisting, like the latter, of layers of connective tissue, though somewhat modified, both structurally and chemically, since it is transparent, admitting light into the interior of the eye, and yielding chondrine on boiling. The cornea may be described as consisting of three parts: a stratified epithelium anteriorly, continuous with that of the conjunctiva, a middle portion, the cornea proper, continuous with the sclerotic, consisting of modified connective tissue, posteriorly, of a homogeneous, elastic lamella, covered with epithelium-like cells, the membrane of Demours or Descemet, the part of the membrane passing to the anterior surface of the iris,

[1] Traite d'Anatomie, Tome troisieme, p. 747. Paris, 1877.

more noticeable in the eyes of the sheep and ox than in man, being known as the ligamentum pectinatum iridis. In a state of health in the adult, vessels are not found in the cornea, except at its circumference, where they are disposed in capillary loops, and by

FIG. 427.



Horizontal section of right eyeball. 1. Optic nerve. 2. Sclerotic coat. 3. Cornea. 4. Canal of Schlemm. 5. Choroid coat. 6. Ciliary muscle. 7. Iris. 8. Crystalline lens. 9. Retina. 10. Hyaloid membrane. 11. Canal of Petit. 12. Vitreous body. 13. Aqueous humor.

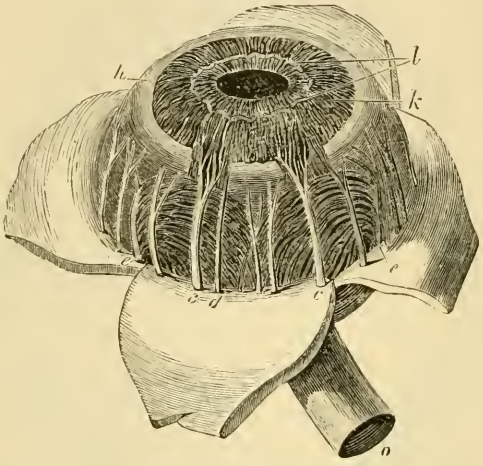
which nutrition is apparently carried on. The nerves of the cornea are, however, very numerous, and are derived from the long and short ciliary nerves. Entering the sclerotic, and crossing the choroid, they pass into the cornea, extending almost through to its free surface.

The Choroid.

Removing the sclerotic in the manner represented in Fig. 428, the second coat of the eyeball from without inward, the choroid with its anterior prolongation, the ciliary muscle will then be exposed. The choroid may be regarded essentially as the vascular pigmental tunic of the eyeball. Its inner or pigmental layer constitutes, however, in reality, the outer coat of the retina, being developed, as we shall see hereafter, like the latter from the invaginated portion of the optic vesicle. The choroid, varying in thickness from the $\frac{1}{6}$ mm. to 1 mm. ($\frac{1}{150}$ to the $\frac{1}{25}$ of an inch), and covering the eyeball to the same extent as the sclerotic, is connected by its outer surface with the latter tunic by connective tissues, vessels, and nerves, the so-called membrana fusca, and, like the sclerotic, is traversed posteriorly by the optic nerve. The arteries

of the choroid, the short ciliary, comparatively large after piercing the sclerotic close to the optic nerve, break up into branches, which pass forward and then inward to end in the capillaries, the latter being sometimes known as the tunic of Ruysch. The veins situated externally to the other vessels are very numerous, and, being

FIG. 428.



Choroid membrane and iris exposed by the removal of the sclerotic and cornea. Twice the natural size. *a*. One of the segments of the sclerotic thrown back. *l*. Ciliary muscle. *k*. Iris. *e*. One of the ciliary nerves. *f*. One of the vasa vorticosa or choroidal veins. (QUAIN.)

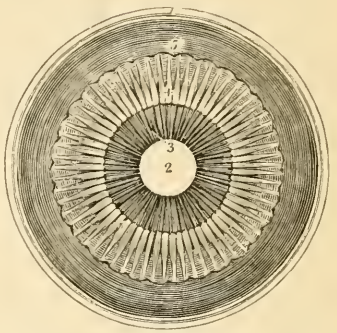
disposed in curves converging into four trunks, present a peculiar appearance, which has given rise to the name of vasa vorticosa. Among the vessels of the choroid are also found elongated and stellated pigment cells, with branches, which, intercommunicating, constitute a sort of network. The nerves supplying the choroid are derived from the long and short ciliary. The inner surface of the choroid is smooth and is covered with the hexagonal pigmental cells of the retina, which will be considered as the outer layer of that tunic rather than, as formerly, as the inner layer or tapetum nigrum of the choroid for the reason just given.

Ciliary Processes.

It will be observed from Fig. 428 that the choroid passes forward into the ciliary muscle, the latter in turn passing into the iris, constituting, in fact, one continuous layer—the second tunic of the eyeball. If, however, the choroid be viewed from behind, as represented in Fig. 429, in which the eyeball is supposed to have been divided transversely, it will be seen that the choroid passes forward and posteriorly into the ciliary processes, just as we have seen it passes forward but anteriorly into the ciliary muscle. Or, briefly, the relation of the parts may be expressed by saying that the choroid splits at its anterior termination into the ciliary muscle

in front, and the ciliary processes behind, the ciliary muscle being continued into the iris, hence the general term of uvea applied to all of these parts by the older anatomists. The ciliary processes or plications, about seventy in number, disposed radially behind the ciliary muscle and the iris, and fitting posteriorly, as we shall see, into corresponding plications of the suspensory ligament of the lens, more particularly into that part of it known as the zone of Zinn, consists of large and small thickenings of the choroid, the small folds alternating, though irregularly, with the large ones, the latter measuring about the $\frac{1}{10}$ of an inch in length and the $\frac{1}{40}$ in depth, and composed like the choroid proper of vessels and pigment, the latter, though, being absent in the rounded inner ends.

FIG. 429.



Ciliary processes as seen from behind. 1. Posterior surface of the iris, with the sphincter muscle of the pupil. 2. Pupil. 3. One of the ciliary processes, of which about seventy-one are represented. ½. (QUAIN.)

Ciliary Muscle.

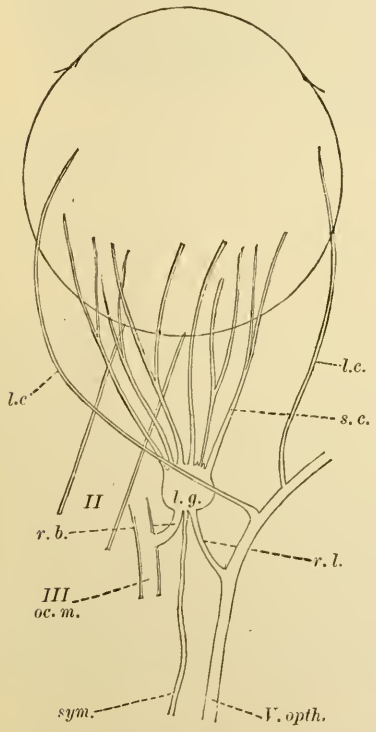
The ciliary muscle (Fig. 428, *b*), the continuation anteriorly of the choroid, about 3.1 millimeters ($\frac{1}{8}$ of an inch) wide, consisting of longitudinal and circular fibers, the latter, however, present at the periphery of the iris only, may be regarded as arising from the inner side of the junction of the sclerotic and cornea, close to the canal of Schlemm, and inserted into the choroid opposite the ciliary processes. Such being its disposition, it is evident that, in contracting, the nerves supplying it being the long and short ciliary nerves, it will draw the choroid forward, thereby compressing the vitreous humor and relaxing the suspensory ligament of the crystalline lens, the significance of which action will be better appreciated when the subject of accommodation has been considered.

The Iris.

The iris (Fig. 428, *c*), the circular, contractile, and colored membrane seen through the transparent cornea, to which the characteristic color of the eye is due, is the muscular diaphragm of the eye, the aperture in its center or pupil permitting and regulating the passage of light into the interior of the eye. The iris, about as thick as the choroid, is attached by its circumferential border to the line of junction of the cornea and sclerotic at the origin of the ciliary muscle, and measures about one-half an inch across, and in a state of rest about the one-fifth of an inch from the circumfer-

ence to the pupil. The iris consists essentially of a stroma of connective tissue and muscular fibers, the latter disposed as a ring around the pupil, constituting the sphincter, and as a rays from the center to the circumference, the dilator muscles of the iris. The pupil, or aperture in the iris regulating the amount of light admitted, varies in size according as the muscular fibers are contracted or relaxed, from the one-twentieth to the one-third of an inch, and during fœtal life is closed by a delicate transparent membrane. The iris is supplied by the two long ciliary and anterior ciliary arteries, the latter being derived from the muscular branches of the ophthalmic.

Fig. 430.



Diagrammatic representation of the nerves governing the pupil. *II.* Optic nerve. *l. g.* Lenticular ganglion. *r. b.* Its short root from *III. oc. m.* Third or oculomotor nerve. *sym.* Its sympathetic root. *r. l.* Its long root from *V. ophthm.*, the nasal branch of the ophthalmic division of the fifth nerve. *s. c.* The short ciliary nerves from the lenticular ganglion. *l. c.* The long ciliary nerve from the nasal branch of the ophthalmic division of the fifth nerve. (Foster.)

The two long ciliary arteries having pierced the sclerotic, one on each side of the optic nerve, pass between the latter tunic and the choroid to the ciliary muscle, and each vessel, just before reaching the iris, divides into an upper and lower branch, which, anastomosing with the corresponding vessels of the opposite side, and with the anterior ciliary arteries, forms a vascular ring, the circulus major of the ciliary muscle, from which small branches are given off, some of which supply the muscle, while others, converging toward the pupil, form a second vascular circle — the circulus minor; from the latter capillaries are given off which terminate in veins. The veins of the iris terminate in the circular venous sinus known as the canal of Schlemm, situated at the junction of the cornea with the sclerotic. The nerves of the iris are the long ciliary, which, as we have already seen, are given off from the nasal branch of the ophthalmic and the short ciliary nerves derived from the ciliary ganglion. The ciliary nerves, after piercing the sclerotic, pass forward on the surface of the choroid, to which tunic they give branches, to the ciliary muscle, in which they form a plexus continued forward into the iris; they apparently terminate at the pupil in a plexus of non-medullated fibers. The lenticular or ciliary gan-

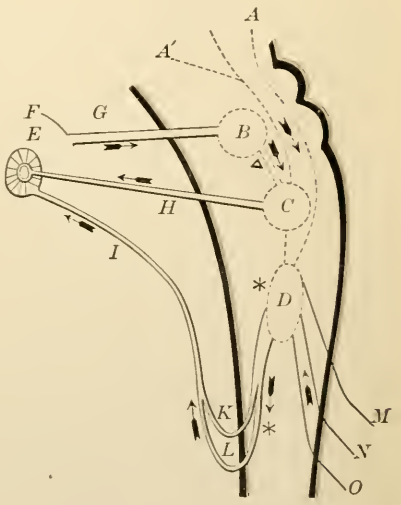
glion (*l. g.*, Fig. 430) being made up of fibers derived from the third pair, the nasal branch of the ophthalmic and the sympathetic, it may be inferred that the short ciliary nerves consist of motor, sensory, and sympathetic fibers.

It has already been mentioned that the fibers of the third pair of nerves and of the sympathetic exercise an antagonistic influence upon the pupil; division of the third pair being followed by dilation, and that of the sympathetic by contraction of the pupil.

Putting together these facts, and further assuming that the fibers of the third pair and sympathetic pass through the ganglion, thence, as the ciliary nerves, to terminate in the circular and dilator fibers of the iris respectively, it has been supposed that the pupil dilates if the third pair be divided, since there is nothing then to antagonize the dilating effect of the sympathetic, and that the pupil contracts if the sympathetic be divided, since then there is nothing to antagonize the constricting effect of the third pair.

Recent investigations[1] render it probable, however, that the impulses that cause dilation of the pupil are transmitted by those fibers of the sympathetic that, passing over the ganglion of Gasser, run juxtaposed with those of the ophthalmic branch of the fifth nerve, and thence through the nasal branch of the latter into the long ciliary nerve, rather than by those fibers that pass, as just mentioned, into the ciliary ganglion. Such being the disposition of the nerves innervating the muscular fibers of the iris, it may be said that the contraction of the pupil due to the falling of light upon the retina is a reflex act, the optic being the afferent nerve, the third the efferent nerve, the center that part of the floor of the aqueduct beneath the anterior corpora quadrigemina. (Fig. 431.) That this is the case, is shown by the following facts: When the optic nerve is divided (it being supposed that the observation is limited to one eye), light falling on the retina of that eye no longer causes

Fig. 431.



Schema of the nerves of the iris. *B, C.* Oculomotor center. *D.* Dilator center. *E.* Iris. *G.* Optic nerve. *H.* Oculomotor (contractor) nerve. *I.* Sympathetic (dilator) nerve. *K, L.* Anterior roots. *M, N, O.* Posterior roots. Δ. Seat of lesion, causing pupillary immobility. *. Probable seat of lesion, causing myosis. (Landois.)

[1] Langley, Journal of Physiology, Vol. xiii., p. 575.

contraction of the pupil. When the third nerve is divided, stimulation of the retina, or of the optic nerve, does not cause contraction of the pupil, whereas stimulation of the peripheral end of the divided third nerve may cause extreme contraction. If the center beneath the corpora quadrigemina be stimulated, the pupil will contract, even though no light falls upon the retina or after division of the optic nerve, whereas after destruction of the center, stimulation of the retina will not cause contraction of the pupil. Finally, the center and its connections with the optic and third nerves being intact, light falling upon the retina will still cause contraction, even though all the other parts of the brain have been removed.

It should be mentioned, however, in this connection, that light, apart from any nervous influence, will exercise a direct stimulating effect upon the iris, causing the pupil to contract even after the eye has been removed from the orbit several hours after death.

This fact is an important one, since it offers an explanation of the pupil contracting at times even after division of the third nerve. The contraction of the pupil in response to the direct stimulus of light is, however, a very different one from that observed when the action is a nervous reflex one, taking place only after a very long exposure. While there is still some doubt as to exactly how the fibers of the optic nerves are connected with the pupil constrictor center, it appears to have been established that the constricting impulses are transmitted by those fibers of the third nerve that arise in the anterior part of the nucleus, close behind those influencing accommodation, the fibers arising from the posterior part innervating the ocular muscles. While contraction of the pupil in response to the stimulus of light acting in the manner just mentioned, appears to be understood, difference of opinion still prevails as to how dilation of the pupil is caused. According to some physiologists, the dilation of the pupil is a vasomotor phenomenon, being due to contraction of the blood vessels. That such is not the case, however, is shown by the following facts: That stimulation of the long ciliary nerves causes dilation of the pupil without contraction of the blood vessels of the iris, and that stimulation of the sympathetic after division of the long ciliary nerves, causes contraction of the blood vessels, without dilation of the pupil. The fibers of the long ciliary nerves, which appear to transmit the impulses which cause dilatation of the pupil, pass down the cervical sympathetic (Fig. 431, *D*) to the upper thoracic ganglion, and by the ramus communicans and anterior root of the second thoracic nerve into the spinal cord, and thence upwards to the pupil dilator center (Fig. 431, *C*), situated in the aqueduct close to the pupil constrictor center. A secondary pupil dilator center, the so-called cilio-spinal center, is also supposed by some physiologists to exist in the cord just

above the level of the second thoracic nerve. The pupil dilator center of the medulla appears to be excited by emotions such as fear, by the stimulation of sensory nerves, dyspnœa, etc., and as contraction of the pupil follows nerve division of the sympathetic, the center seems to be a tonic one constantly sending impulses to the dilatory fibers of the iris. It appears, therefore, that it is by the oculo-motor mechanism, that the size of the pupil is modified according to the amount of light, and that by means of the sympathetic the pupil is influenced by other stimuli. The reflex dilatation of the pupil follows a little later than the reflex contraction, the time intervening between the cutting off of the light and stimulating by the same being 0.5 and 0.3 sec. respectively. The pupil reflex in man and many of the higher animals is a bilateral one, that is to say, light falling upon the retina of one eye causes contractions of the pupils of both eyes. Any one can convince himself that such is the case by illuminating the retina of one eye by means of light transmitted through a pinhole in a screen placed in the anterior focus and then alternately closing and opening the other eye, the size of the circle of light being increased or diminished accordingly. The bilateral character of the pupil reflex appears to depend upon the extent of the decussation of the optic fibers in the chiasma, since in those animals in which decussation is complete, the contraction of the pupil is confined to the illuminated eye. Further, as we have just seen that the extent of the decussation is associated with the position of the eyes in the head, it will be found that in animals having binocular vision the pupil reflex is bilateral.[1]

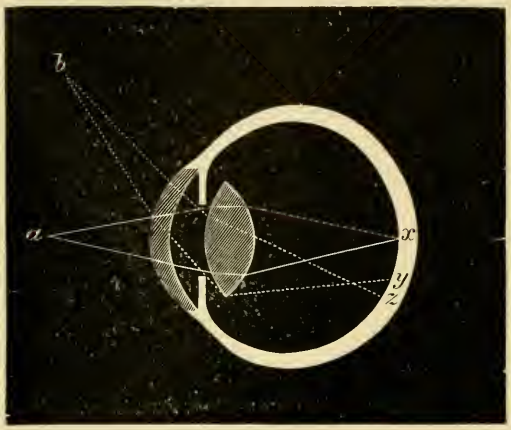
Of the light that enters the eye part is absorbed by the black pigment, part reflected and in the same direction in which it enters. In observing the eye of another person the head of the observer, being an opaque object, cuts off the light and as no light therefore enters the eye, none is reflected back. Hence the pupil of the eye appears to one observing it as a black circular spot in the middle of the colored iris. It is obvious, therefore, that in order to see the interior of the eye the latter must be illuminated by lateral rays the eye of the observer being in the line of vision. It is upon these principles that is based the construction of the ophthalmoscope the nature of which will be however better understood after the action of lenses upon light has been explained.

While the function of the iris is without doubt that of a diaphragm, regulating, through the pupil, the amount of light admitted to the interior of the eye, it will be observed, from

[1] In the case of owls in which the visual axes are parallel, difference of opinion still prevails as to the extent of the decussation of the optic fibers. Thus, while according to Ferrier (Croonian lecture, 1890, p. 70), decussation is incomplete, according to Steinach (Pflüger's Archiv, B. 47, s. 313), it is complete and the pupil reflex unilateral as in other birds.

Fig. 432, that not only will the light enter the eye from a point (a) in the line of direct vision, but from a point (b) outside that

Fig. 432.



Diagrammatic section of the eyeball, showing difference of refraction for direct and indirect vision. a, x. Rays from a point in the line of direct vision, focussed at the retina. b, y, z. Rays from a point outside the line of direct vision, brought to a focus and dispersed before reaching the retina. (Dalton.)

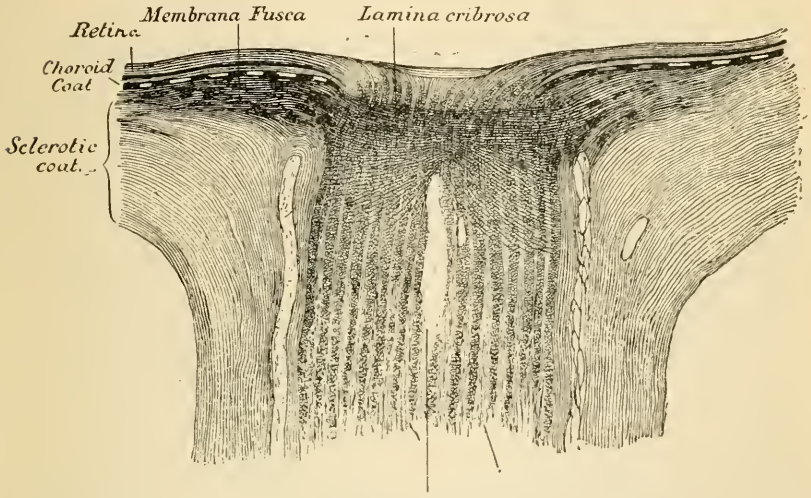
line, and that the latter rays being brought too soon to a focus, are dispersed again before reaching the retina, and so give rise to confused vision.

The Retina.

If the choroid, including the tapetum nigrum, be removed under water in the same manner as the selerotic, the third tunic of the eye from without inward, or the retina, will be then exposed as a very delicate and transparent membrane, through which will be seen the posterior portion of the underlying vitreous humor. Within a short time after death, however, the retina loses its transparency and becomes opaline, the change being hastened by the action of water, alcohol, and other fluids. The retina, varying in thickness from $\frac{1}{2}$ to $\frac{1}{8}$ of a millimeter ($\frac{1}{50}$ to $\frac{1}{200}$ of an inch), extends over the posterior portion of the eyeball to within a distance of about 1.4 millimeters ($\frac{1}{18}$ of an inch), of the ciliary processes, and, if torn from its anterior attachment, presents a finely indented edge, the so-called ora serrata. As a matter of fact, however, the retina does not terminate, as often said, at the ora serrata, but is continuous forward as a thin layer of transparent columnar nucleated cells, the pars ciliaris retinæ, which, reaching the tips of the ciliary processes, then disappears. The retina, the nervous tunic of the eye, and that portion of it susceptible of being impressed by light, may be regarded as an expansion of the optic nerve, though it is usually described as being traversed by the latter, like the selerotic and choroid. The optic nerve apparently, then, penetrates the

retina about 3 millimeters ($\frac{1}{8}$ of an inch) within, and 1 millimeter ($\frac{1}{25}$ of an inch) below the antero-posterior axis of the eye. The nerve fibers being at this point, the porus opticus, slightly elevated, gives rise to a small eminence (Fig. 433), the colliculus nervi optici,

FIG. 433.

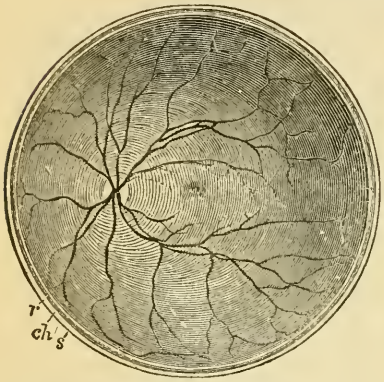


Section through the middle of the optic nerve and the tunics of the eye at the place of its passage through them. (ECKER.)

between which the central artery of the retina appears, and spreads out arborescent-like, over the inner surface of the retina (Fig. 434), and the branches of the central veins converge and disappear. To the outer side of the optic nerve, about 2.5 millimeters ($\frac{1}{10}$ of an inch), may be also seen on the inner surface of the retina, a yellow spot, somewhat elliptical in shape, about 3 millimeters ($\frac{1}{8}$ of an inch) long, and 0.8 millimeters ($\frac{1}{36}$ of an inch) broad, its long diameter being horizontal, the so-called macula lutea or limbus lutens of Sömmering, presenting in its center a depression, the fovea centralis, which is situated in the axis of vision. As the retina is so thin at this point that the pigmental layer can be seen clearly behind it, the fovea centralis gives the impression that it is a hole that has been made in the retina. It is an interesting fact, that the yellow spot of Sömmering has only been found in the eye of the primates. The sensitiveness of the retina to light varies very much, being greatest at the yellow spot, and gradually diminishing toward the periphery. The difference can be determined experimentally on the same principle as the tactile sensibility of the skin was determined. Thus, if two wires be placed close together, but sufficiently far apart to enable us to distinguish one from the other, and then the eye be so directed that the image of the wires shall fall, first upon the yellow spot, and then upon the great circle of the eye ; in the latter case,

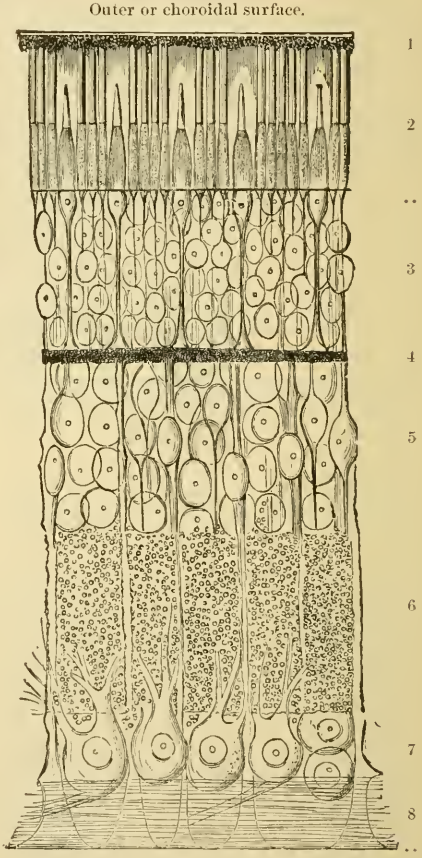
the wires, to be seen distinctly, must be separated at a distance 150 times greater than in the former one. It is evident, therefore, why the movements of the eyeball all tend to bring the image of external objects upon the yellow spot, and as the latter only constitutes about the $\frac{1}{500}$ of the retina, it follows that but a small portion of

FIG. 434.



The posterior half of the retina of the left eye viewed from before. Twice its natural size. *s*. Cut edge of the sclerotic. *ch*. Choroid. *r*. Retina: in the interior at the middle the macula lutea with the depression of the fovea centralis is represented by a slight oval shade; toward the left side the light spot indicates the colliculus or eminence at the entrance of the optic nerve, from the center of which the arteria centralis is seen sending its branches into the retina, leaving the part occupied by the macula comparatively free. (HENLE.)

FIG. 435.



Diagrammatic section of the human retina. 1. Layer of the pigment cells. 2. Layer of rods and cones. . . Membrana limitans externa. 3. Outer nuclear layer. 4. Outer molecular layer. 5. Inner nuclear layer. 6. Inner molecular layer. 7. Layer of nerve cells. 8. Layer of nerve fibers. . . Membrana limitans interna. (SCHULTZE.)

the latter is actually made use of in distinct vision. As an illustration may be mentioned the familiar fact that, in reading, we see one or two words at a time, and that the eye must pass over the whole line in order to read it.

The retina consists, microscopically, of a connective tissue scaffolding, so to speak, supporting eight distinct layers disposed from without inward, as follows (Fig. 435): 1, pigmentary layer; 2, columnar layer; 3, outer nuclear layer; 4, outer molecular layer; 5, inner nuclear layer; 6, inner molecular layer; 7, ganglionic layer; and 8, nerve layer. The first outer, or pigmentary, layer of the retina, formerly described as the inner layer, or tapetum nigrum of the choroid, consists of a single stratum of hexagonal nucleated epithelium cells. The outer surface of each

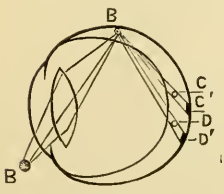
cell, that lying next to the choroid, is smooth, flattened, and usually free from pigment; the inner portion, prolonged as fine straight filamentous processes between the rods and cones of the second or columnar layer is, however, loaded with pigment. The second, or columnar layer, also known as the bacillary layer, Jacob's membrane, consists of millions of elongated bodies, the so-called rods and cones, disposed, in a palisade-like manner, between the pigmentary layer and the so-called membrana limitans externa, which is not a continuous membrane, but is formed through the connective tissue fibers of the retina uniting more or less along a definite line at the boundary of the third, or outer nuclear layer. The rods exceed the cones in number, the latter amounting to more than three millions, there being usually about four rods to one cone, except at the macula lutea, where cones only are present; they have an elongated cylindrical form with a diameter of about $\frac{1}{500}$ of a millimeter ($\frac{1}{12500}$ of an inch) and a length of $\frac{1}{20}$ of a millimeter ($\frac{1}{506}$ of an inch). The cones on the other hand, are shorter and thicker, having a diameter of about $\frac{1}{164}$ of a millimeter ($\frac{1}{4166}$ of an inch), bulge out at the inner end or base, and terminate externally by a fine tapering portion. The cones are usually separated by a distance of $\frac{1}{100}$ of a millimeter ($\frac{1}{2500}$ of an inch), the intervening portion being filled by rods.

Through delicate fiber-like prolongations the inner ends of the rods and cones are in relation with the third or outer layer of the retina, the outer nuclear layer, which consists of several strata of clear, oval elliptical nucleated cells from both ends of which delicate fibers are prolonged. These outer cells, presenting marked differences, are of two kinds, known as rod granules and cone cells, according as they are connected with the rods or cones, respectively. While the outer fibers of the outer nuclear layer are prolonged into the rods and cones, the inner fibers of the same are prolonged into the outer molecular layer; the latter in turn appears to be in relation through fibrils with the cells of the inner nuclear layer, the latter being in relation with the inner molecular layer.[1] The seventh layer of the retina from without inward, the ganglionic or layer of nerve cells, consists of a stratum of nerve cells of a spheroidal or pyriform figure, which appears to be in relation by fibers on the one hand, with the preceding inner molecular layer, and, on the other, with the fibers of the optic nerve. The latter, constituting the eighth layer of the retina, appears to be bounded by a distinct membrane, the membrana limitans interna, which, however, is not a continuous structure, as its appearance would lead one to suppose, but is formed, like that of the membrana limitans externa, by the terminal fibers of the sustenacular or connective tissue framework of the retina being united together at this point. From this necessarily brief description of the minute structure of the retina it will be seen that the layer of the rods and cones, or Jacob's mem-

[1] Rauber, op. cit., s. 723. Gehuchten, op. cit. s. 628.

brane, bounded externally by the pigmentary layer, may be regarded as the termination of the optic nerve fibers. It may be mentioned, in this connection, that, as the rods and cones far exceed the optic nerve fibers in number, it is impossible that each optic nerve fiber should be connected with a rod or cone throughout the retina, though such a relation may exist at the macula lutea. It has already been mentioned that at the macula lutea the rods are absent, the cones only being present; the latter are, further, much longer and narrower than elsewhere, especially opposite the fovea. At this portion of the retina the various layers of which it consists are also very much thinned. The yellow color of the macula, deepest at the center, is due to a coloring matter diffused through all the layers except that of the cones and the outer nuclear layer. It might naturally be supposed that the anterior layer of the retina, that facing the light, would be the sensitive layer—as a matter of fact, of all the layers of the retina, however, that of the rods and cones is most sensitive to light, as can be shown experimentally by so illuminating the eye that one is able to perceive the shadows of the vessels of his own retina, which are cast upon the layer of rods and cones. The vessels of the retina, being situated in its anterior layer, necessarily cast their shadows on one of its posterior layers, and the only reason that we do not ordinarily see these shadows is probably that we have become so accustomed to them that they no longer attract our attention. If, however, the source of light be placed in an unusual position, as in Fig. 436, then the shadows of the vessels falling on an unusual portion of the layer of rods and cones will be perceived, and will be seen by one looking at a very dark surface in a dark room, as if projected at D′ C′, and resembling exactly the vessels of the retina, the picture of the retina so seen being known as the vascular tree of Purkinje. Now it was shown by H. Muller,[1] that the distance between the anterior layer of the retina, and the layer of rods and cones was about equal to that between the retinal vessels and their shadows; necessarily, then, the layer of rods and cones must be sensitive to light. Now, it being remembered that the layer of rods and cones lies next to the pigmental layer, and that the retina, with the exception of the latter layer, is transparent, it follows that a ray of light passes through the retina until it reaches the pigmental layer when it ceases to be light, being transformed into either heat, chemical or nervous force; the latter exciting the rods and cones, gives rise to an impression which is then transmitted

Fig. 436.



B. A candle placed at the side of the eye—that is, as much to the side of the center of the cornea as possible. B′. Interior luminous source, formed by the rays of light concentrated by the crystalline lens upon the extreme lateral portion of the eye. CD. Two vessels of the retina (the size of the retina is here greatly exaggerated). The shadow of these two vessels is seen as if projected at D′ and C′. Experiment of Purkinje.

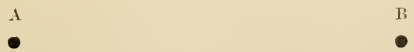
[1] Verhand. der physik. med. Gesellschaft zu Würzburg, v., s. 411.

back to the optic fibers on the anterior surface of the retina, where it is again reflected along the optic nerve fibers to the optic lobes, etc.

It has been shown more particularly by the researches of Kühne[1] that the outer ends of the rods of the retina contain a substance known as "rhodopsin" or "visual purple" and which is apparently elaborated out of the retinal epithelium lying between the rods and cones. If an eye after excision or in its natural position be protected from light for a time, and then the light of a lamp or a window, for example, be allowed to fall upon it, the retina will show, if examined under red light, the image of the object impressed upon it by the bleaching of the purple. If the retina be further treated with a 4 per cent. solution of alum-potash before the retinal epithelium has had time to obliterate the bleaching effects, the image or "optogram" of the external object may be "fixed" as the photographers express it. Even if it be admitted that the chemical changes undergone by the visual purple, due to light act as a stimulus to the optic nerve fibers, such changes cannot be essential to vision, since vision is most acute at the yellow spot just where the visual purple is absent, the rods not being present in that situation. Moreover, vision is fairly distinct in albinos in which the visual purple is absent.

Beyond the statement that the rods and cones are excited by the heat or nerve energy, or whatever the form of energy may be into which the light is transformed in the pigmental layer, little can be said as to the special *rôle* they play in vision. Such facts, however, as that in the bat, hedgehog, and mole, nocturnal animals, and night birds, also, the retina consists solely of rods; whereas, in day-birds, especially in those which live on insects, of brilliant colors, the retina contains a much larger number of cones than the mammalia, would lead one to suppose that the rods are affected by differences in the intensity of the light, the cones by differences in its quality—that is, its color. While there can be no doubt that the fibers of the optic nerve transmit luminous impressions, or their modifications, in the manner described, it can be shown experimentally that the part of the retina where these fibers appear is insensitive to light, and is called, for that reason, the punctum cæcum. Thus, if two black points (Fig. 437, A, B), on a piece of paper, separated

FIG. 437.



by a distance of two inches, be viewed at a distance of six inches by the right eye, the left eye being closed, the point B will be invisible, being then opposite the punctum cæcum, or blind spot.

[1] Centralbl. f. d. med. Wissensch., 1877, s. 194. Hermann, op. cit., Bd. 3, 1, 1879, s. 261.

The Vitreous Humor and Hyaloid Tunic.

The vitreous humor, while enclosed by the retina, does not, however, lie loosely in the cavity of the eyeball, being invested by a delicate membranous capsule, about $\frac{1}{240}$ of a millimeter ($\frac{1}{6000}$ of an inch) in thickness—the hyaloid tunic. The latter is thicker in advance of the retina than elsewhere, and, as already mentioned, is impressed by the ciliary processes of the choroid, the zone so formed around the crystalline lens, and well defined by the staining of the processes, being known as the zone of Zinn. Anteriorly the hyaloid tunic splits into two laminæ, which, diverging at the border of the crystalline lens, becomes confluent with the anterior and posterior surfaces of its capsule, the two laminæ adhering at intervals; if the space between them be inflated, it will assume the appearance of a beaded canal, surrounding the circumference of the lens—the canal of Petit. Such being the disposition of the hyaloid tunic, it is evident that not only does it support the vitreous humor, through investing the latter, but acts also, from what has just been said, as the suspensory ligament of the lens. The vitreous humor, one of the refractory media of the eye, occupying about the posterior two-thirds of the globe, consists of a clear, glassy, gelatinous matter, containing albumin, a mucoid, and mineral bodies. It is divided into compartments by delicate membranous processes, which, given off by the hyaloid tunic, penetrate its substance. The specks that one sees occasionally floating about, as it were, in the field of vision, the so-called muscæ volitantes, are due to the shadows cast upon the retina by the connective tissue elements suspended in the vitreous humor.

The Crystalline Lens.

The crystalline lens (Fig. 427, 8), the most important of the refracting media of the eye, transparent and very elastic, is situated in the hyaloid fossa of the vitreous humor, behind the pupil, and is enclosed, as already mentioned, between the laminæ of the hyaloid tunic, the latter constituting its suspensory ligament. The crystalline lens is a double convex lens, the convexity of the posterior surface being greater than that of the anterior. The antero-posterior diameter, 6.2 millimeters ($\frac{1}{4}$ of an inch), is, however, a little less than that of the lateral one, 8.3 millimeters ($\frac{1}{3}$ of an inch). With advance in age the convexities diminish, the lens becomes harder and inelastic, which accounts for the gradual diminution in the power of accommodating the eye to distances. If the lens be examined with a low magnifying power, there will be observed on each of its surfaces a star-like body, nine or sixteen rays of which extend from the center to within about two-thirds of the periphery. The body of the stars and their rays are not of a fibrous character, like the rest of the lens, but consist of a homogeneous substance, which extends between the fibers. The latter are flattened, six-sided prisms, from $\frac{1}{192}$ to $\frac{1}{86}$ of a millimeter ($\frac{1}{4800}$ to $\frac{1}{2400}$ of an

inch) broad, and from $\frac{1}{520}$ to $\frac{1}{360}$ of a millimeter ($\frac{1}{13000}$ to $\frac{1}{9000}$ of an inch) thick. Their flat surfaces are parallel with the surface of the lens, and their direction is from the center, and from the rays of one star to the periphery, where they turn and pass toward those of the other. Chemically, the lens is composed of a globulin, called crystalline, combined with inorganic salts. The crystalline lens is enclosed within a very thin, transparent, elastic membrane, the capsule, which is lined anteriorly with a layer of delicate nucleated cells.

The Aqueous Humor.

The aqueous humor (Fig. 427, 13), the remaining of the refracting media of the eye, is a colorless, transparent, almost watery fluid, filling the anterior chamber of the eye—that is, the space between the cornea in front and the iris and crystalline lens behind, and the posterior chamber, or the space between the posterior surface of the iris and the lens, supposing that such a place exists, which is very doubtful, and in any case must be very small. That the aqueous humor is secreted possibly by the blood vessels of the iris and ciliary processes, or the internal layer of the cornea, is shown by the rapidity with which it is reproduced after it has been evacuated, as in surgical operations performed upon the eye. The solids of the aqueous humor amount to thirteen per thousand, among which serum globulin and globulin are found in traces.

Intraocular Pressure.

The watery fluids filling the cavity of the eye are during life subjected to a pressure, the so-called intraocular pressure. This pressure, depending upon that of the blood pressure of the retina, choroid, etc., must vary with the latter, rising and falling with it. The character of this pressure is determined by pressing upon the eyeball and of so learning whether it is soft, tense, or compressible.

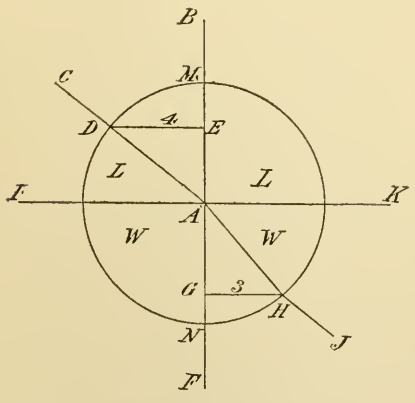
CHAPTER XXXIX.

PHYSIOLOGICAL OPTICS.

Refraction and Accommodation.

From the necessarily brief description just given of the eye, it is apparent that it resembles essentially in its structure the camera of the photographer, its refractive media being comparable to the lens, the iris to the diaphragm, the choroid to the internal blackened surface, the retina to the sensitive plate, the image of the external object being brought to a focus on the retina or sensitive plate, respectively, through the refraction undergone by the rays of light. In order, however, to understand the manner in which the rays of light are brought to a focus on the retina by the cornea, crystalline lens, etc., it will be necessary to describe briefly the phenomena of refraction or the course that rays of light take in passing through refractive media. Suppose that *W W* (Fig. 438) represent a mass of water, and *C A* the direction of a beam of light passing through the atmosphere *L L*, the rarer medium, it will be observed that as the ray of light passes through the water, the denser medium, it is bent toward the perpendicular *A F*, but that as it passes out of the water into the air again, the rarer medium, it is bent away from the perpendicular. Let now the line *C A*, representing the direction of the incident beam, be connected with the perpendicular *B F* by the line *D E*, and the line representing the refracted beam *A H*, be connected with the perpendicular by the parallel line *G H*, and it will be seen that the line *G H* is three-fourths as long as the line *D E*; and further that this ratio of 4 to 3, equal to 1.336, will be invariably the, same whatever the angle may be that the incident beam *C A* makes with the surface of the water *I K*, except it be a right angle, the beam then passing directly through the water without being refracted at all.

Fig. 438.



Refraction of Light.

The well-known fact of a stick appearing bent when obliquely

thrust into water (Fig. 439) or of a coin lying upon the bottom of a vessel appearing to be at some distance from the latter (Fig. 440), are familiar illustrations of refraction.

Fig. 439.

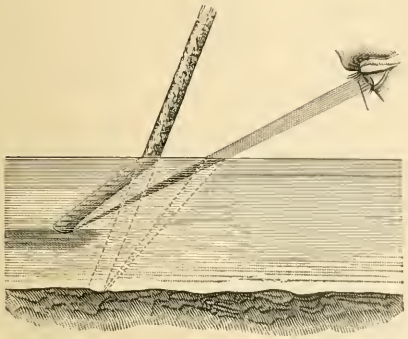


Illustration of refraction.

Fig. 440.

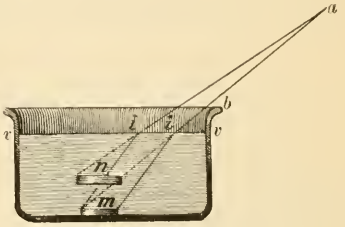


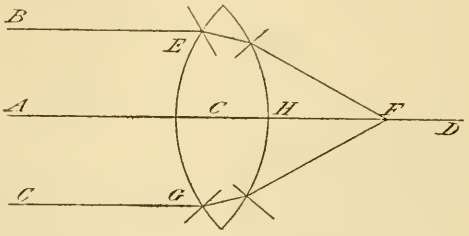
Illustration of refraction.

If, however, with A as a center, and a radius $A\ D$, a circle be described, the line $D\ E$ becoming then trigonometrically the sine of the angle $D\ A\ M$, and the line $G\ H$ the sine of the angle $H\ A\ N$, the law according to which light is refracted as it passes from air through water, may be expressed by saying, that the ratio of the sines of the angles of incidence and of refraction equals $\frac{4}{3} = 1.336$ and is constant for the particular substance water, or, briefly, that the index of refraction of water is 1.33. That is to say, if the line $D\ E$ is 4 inches in length, then $H\ G$ will be 3 inches, the two being always in the same ratio. If now, for water, crown glass be substituted, it will be found that the sine of the angle of incidence $D\ E$ is to the sine of the angle of refraction $H\ G$ not as 4 is to 3, as in the case of air and water, but as 3 to 2—that is, the index of refraction for the particular substance crown glass equals $\frac{3}{2} = 1.5$.

Bearing in mind then, that as the beam of light passes from the air, the rarer medium, through the glass it is bent toward the perpendicular, but away from it as it passes out of the glass, the denser medium, and that by the index of refraction is meant the ratio of the sines of the angles of incidence and refraction, there will be no difficulty in comprehending the manner in which the direction of a beam of light is altered in passing through biconvex and biconcave lenses. Let C (Fig. 441), for example, represent a biconvex lens of crown glass in which the radii of curvature are nearly equal—that is to say, the two surfaces or curves of the lens are about equally distant from the centers of the circles of which these curves form parts, and that $B\ E$, $C\ G$ be two luminous rays parallel with the principal axis $A\ D$ passing through the optical center C of the lens, which fall upon the lens at the points E and G, respectively. Then, according to the law just enunciated, the

ray $B\ E$ being first bent toward the perpendicular, and then away from the perpendicular, and the ray $C\ G$ being in the same manner bent first toward and then away from the perpendicular, and the ray $A\ C$ being in the direction of the optical axis, and consequently

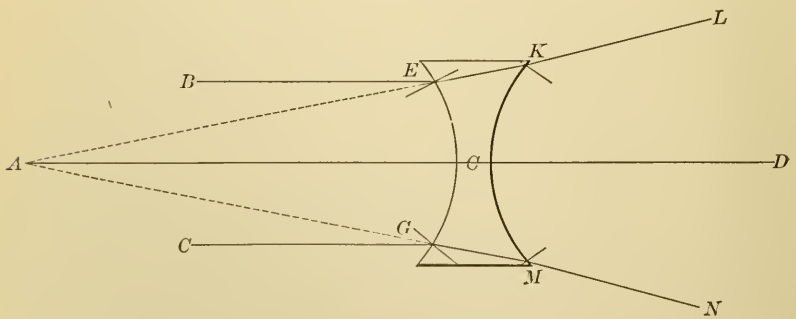
Fig. 441.



Effect of biconvex lens upon rays of light.

passing through the lens perpendicularly, and, therefore, unrefracted, it follows that the three rays, and all others parallel with them, will meet at a point F, known as the principal real focus, and situated in the principal axis of the lens at a distance from the latter ($F\ H$) which will be determined presently, and known as the principal focal distance. The effect of a biconvex lens is then to bring parallel rays of light to a focus on the side of the lens opposite to the source of light, the amount of convergence depending upon the radius of curvature of the lens and its index of refraction, which in this particular case, as we have seen, is 1.5. The converse of this is also true, since if the source of light be at the principal focus F, then the divergent rays after leaving the lens will be brought parallel with each other, and with the principal axis. Such being the action of a biconvex lens, it will be seen from a comparison of Fig. 441 with Fig. 442, that the action of a

Fig. 442.



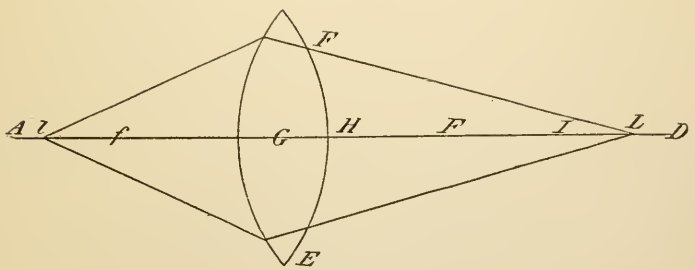
Effect of biconcave lens upon rays of light.

biconcave lens is exactly the opposite of a biconvex one, since the rays of light ($B\ E$, $C\ G$, Fig. 441), after being bent toward their respective perpendiculars and then away from them, according to

the law of refraction, will diverge from the principal axis $A\ D$, instead of converging toward it, and the rays of light $B\ E$, $C\ G$, and all others parallel with them, will diverge as $K\ L$, $M\ N$, instead of being brought to a focus, on the side of the lens opposite to that of the light. In the case of a biconcave lens the focus is negative, virtual, that is to say, it is upon the same side of the lens as the light, and its position is found by prolonging backward the rays $L\ K$ and $N\ M$ until they meet in the principal axis $A\ D$. It will be also observed that the converging rays $L\ K$, $N\ M$ are brought parallel with each other on the same side of the lens as that where the light is now supposed to be.

Let us now consider the case in which the luminous object L is beyond the principal focus F (Fig. 443), but so near that all the incident rays $L\ E$, $L\ F$ form a divergent cone, then, according to the law of refraction, the rays, after leaving the lens, will be found to come to a focus at l, and the converse of this will be found to be true, since, if the luminous object be placed at l, the focus will then be at L, hence l and L are conjugate foci. Further, it will be found by experimentation, or by calculation, that if the distance between the luminous object I and the lens be twice the focal distance—that is, twice $H\ F$ equals $H\ I$—then the focus l will be situated on the other side of the lens at the same distance, or twice $H\ F$, as at the point A, on the axis $A\ D$. If, however, the distance between the lens and the luminous object be less than twice the focal distance, the focus will be situated beyond the point A, and if more than twice the focal distance, then the focus will be situated within the point A—that is, between the point A and the lens. After

FIG. 443.

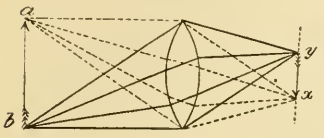


Conjugate foci of lens.

what has just been said, with reference to the manner in which the rays of light are brought to a focus by biconvex lenses, etc., it will be readily seen from Fig. 444 how the image of an object, as of an illuminated arrow, for example, is formed if a biconvex lens be placed between the latter and a screen. It will be observed, however, that the part of the arrow at a being brought to a focus at x, that at b at y, that the image of the arrow is neces-

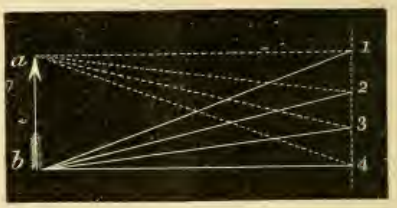
sarily reversed, and that if the luminous object approaches the lens its image recedes and becomes larger, and if it recedes from the lens its image approaches and becomes smaller, and that if the luminous object be situated at twice the focal distance from the lens its image will be of the same size and situated at the same distance from the lens. The distance at which the image is formed behind the lens can be readily calculated in any case by formulæ to be found in any standard work on physics.

Fig. 444.



Paths of rays of light through lens with formation of image.

Fig. 445.



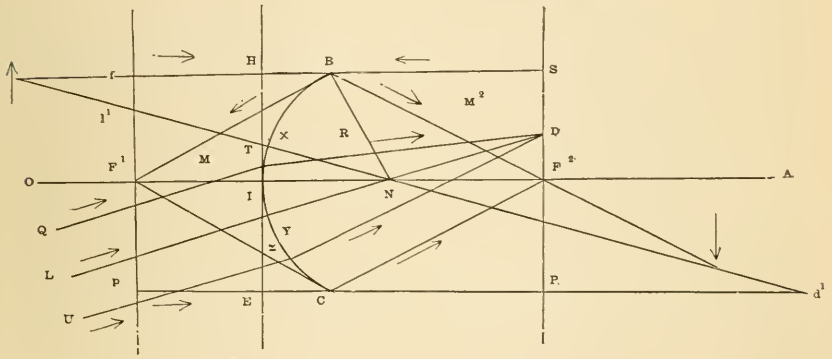
Paths of rays of light without lens.

It need hardly be added that in the absence of a lens, the rays of light will follow the paths indicated in Fig. 445, and as the light from *a* will meet at 4 that from *b*, and the light from *b* at 1 that from *a*, no image of the arrow will be formed upon the screen. Having considered now the properties of lenses, let us apply what has been established of the same to the elucidation of vision, and show how the rays of light, passing successively through the cornea, aqueous humor, crystalline lens, and vitreous humor are finally brought to a focus on the retina.

In considering the paths of the rays of light through the refractive media of the eye physicists make use of a normal schematic eye, a standard eye, so to speak, in which certain cardinal points have been established, and by which the course of the rays of light through the eye can be readily constructed, the position of the focus determined, and the size of the image estimated. Let us endeavor, therefore, to explain the method by which the cardinal points are determined. Let M, M^2 be two refractive media separated from each other by a spherical surface B C (Fig. 446), constituting what is known optically as a simple collecting system, and N the center of curvature —that is, the center of a circle, of which B C forms a part. All the radii drawn from the center N to B C, such as N B, N x, N Y, being perpendicular rays of light falling in the direction of the radii, must pass unrefracted through N as L D, I^1 d^1, for example, and are called, therefore, lines of direction, while N, the point of intersection of all such lines, is called the nodal point. The line O A, connecting N, the center of curvature, with the vertex I, and prolonged in both directions, is known as the optic axis, the plane H E, perpendicular to the optic axis at I, being called the principal plane, and the point I, within the latter, the principal point. Such

being presupposed, it can be shown that all rays parallel with each other, and with the optic axis in the medium M, such as f H, p E, falling upon B C, come to a focus at F^2 in the second medium, called the second principal focus, or second focal point, the plane S F^2 P, perpendicular to the optic axis O A, at this point, being the

FIG. 446.



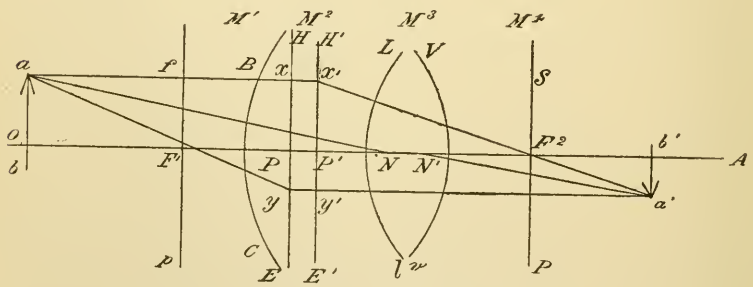
Simple collective system of refracting media.

second focal plane. Of course, the converse of the above is true—that is, rays diverging from F^2, such as F^2 B, F^2 C, pass into the first medium parallel with each other, and with the optic axis. Further, it will be seen from an inspection of Fig. 446, that rays which are parallel to each other in the first medium, but not parallel with the optic axis, such as Q T, U Z, come to a focus in the second medium in the point D of the second focal plane, where the non-refracted directive ray L D meets the latter, and that rays diverging from D pass through the first medium parallel with each other, but not parallel with the optic axis. It is also evident that all rays, which, in the second medium are parallel with each other, and with the optic axis, such as S B, P C, come to a focus (F^1) in the first medium, called the first focal point, or first principal focus, the plane of f F^1 p, perpendicular to the optic axis at this point, being known as the first focal plane. Of course, the converse of the above is true, viz., that rays diverging from F^1 pass through the second medium parallel with each other and with the optic axis.

Finally it follows that the radius of the spherical surface N I is equal to the difference of the distance of the focal points F^1, F^2, from the principal point I—that is, that N I = F^2 I − F^1 I. Such being admitted, it will be seen that an incident ray (Q T) comes to a focus in the second focal plane in the point D, where the non-refracted directive ray L D meets the latter, and that a reversed image ↓ of an external object like an arrow ↑ situated in the first medium is formed in the second medium at the point where the prolonged ray B F^2 meets the non-refracted directive ray l' d'. Now did the eye consist simply of two refractive media, separated

by a spherical surface, as in the simple collecting system just described, the construction of the refracted ray and of the image of the object would be essentially the same and equally simple. Inasmuch, however, as the eye consists of four refractive media, cornea, aqueous humor, crystalline lens, and vitreous humor, the cornea and aqueous humor constituting a concavo-convex lens, the crystalline a biconvex lens, and the vitreous humor a concavo-convex lens, to apply to the eye what has just been established would involve proceeding from medium to medium, which would be a tedious operation. If, however, the several media are centered, that is, if they have the same optic axis, which is pretty nearly the case in the eye, then, as shown by Gauss,[1] the refractive media of such a system may be represented by two imaginary equally strong refractive surfaces (Fig. 447, $P\,P'$), the rays falling upon the first system not being refracted, but projected, so to speak, parallel with themselves to the second surface as at $x\,x'$, $y\,y'$, refraction taking place at the latter just as if that surface alone was present, and that the data required in determining the situation of the two refractive surfaces are the refractive indices of the media, the radii of the refractive surfaces, and the distances of the latter from each other, which can be experimentally determined. Let M^1, M^2, M^3, and M^4 (Fig. 447) be four media,

Fig. 447.



System of refractive media having the same optic axis.

for example, such as the air, aqueous humor, crystalline lens, and vitreous humor; $B\,C$ a spherical surface like the cornea, separating the air from the aqueous humor; $L\,l$ the anterior surface of a biconvex lens like the crystalline lens, a spherical surface separating the aqueous humor from the substance of the lens; and $V\,v$ the posterior surface of the lens, also a spherical surface, reversely disposed, however, with reference to the cornea and anterior surface of the lens, and separating the substance of the lens from that of the vitreous humor. Such being the relation of the refractive media, and the spherical surfaces separating them, the cardinal points of such a system, six in number, are as follows: two

[1] Dioptrische Untersuchungen Abhand. Göttingen Gesells., 1841.

focal points (F' F^2), two principal points (P P'), two nodal points (N N'). Inasmuch as the properties of the two foci F' F^2, as regards the rays of light diverging from or converging toward them respectively, and of the anterior and posterior focal planes $f p$, $S P$, are essentially the same as already described, it will not be necessary to consider them again in detail in this connection. As regards the principal points P P', they being conjugate foci like L l (Fig. 443), rays of light passing through one point will pass through the other also; P P' being the principal points, H E and H' E' will be principal planes, and each point of the one plane having a conjugate focus in the other, a ray of light passing through a point on one plane will pass through a corresponding point on the other at the same distance from the axis and on the same side, the distance F' P being the anterior focal length, and the distance F^2 P' the posterior focal length. In fact, either plane may be regarded as the image, the other being the object. It will be observed that the nodal points N N' are so disposed that if the incident ray a N were prolonged, it would emerge parallel with the emergent ray N' a', and *vice versâ*. Such being the position of the cardinal points in the system of refractive media and spherical surfaces represented in Fig. 447, let a b be an object, an illuminated arrow, for example, from which rays pass through the above; its image will be formed at b' a'. That this must be the case can be at once shown by construction, for the ray a f, after cutting the two principal planes in x x', and passing through the posterior focal points F^2, will meet the line N' a', emerging from the lens parallel with a N, uniting with the latter at the point a', the same point where the ray a F', after passing through the anterior focal point and cutting the principal planes in y y', meets N' a'. In precisely the same manner it can be shown by construction that the point b of the arrow will be brought to a focus at b'. It need hardly be observed that the image of the arrow will be, of course, reversed. Let us suppose now that the index of refraction for air being taken as unity, that with Listing[1] the index of refraction for the aqueous and vitreous humors has been determined to be equal to 1.3379 ($\frac{1}{7}\frac{0}{7}\frac{3}{7}$), that of the crystalline lens to be 1.4545 ($\frac{1}{1}\frac{6}{1}$), the radius of curvature of cornea 8 mm. ($\frac{8}{2\,5}$ of an inch), the radius of curvature of the anterior surface of the crystalline lens 10 mm., that of the posterior surface 6 mm., the distance of the anterior face of the cornea from the anterior surface of the crystalline lens to be equal to 4 mm., the distance from the anterior surface of the lens to the posterior surface, or the thickness of the lens, 4 mm., then by means of appropriate formulæ, developed by mathematical methods[2] from the relations existing between the radii

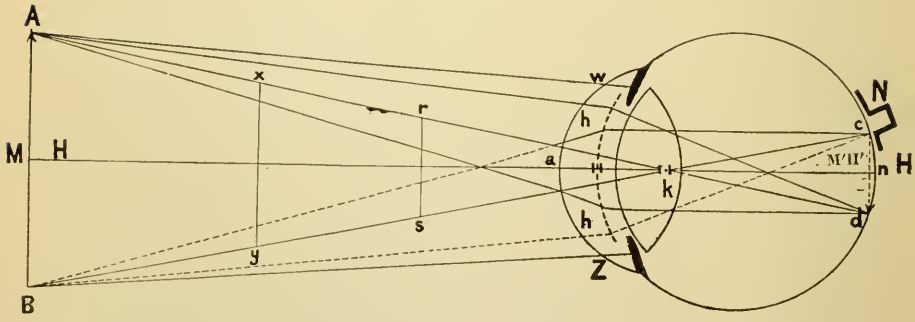
[1] Dioptrik des Auges. Wagner, Physiology, Band iv., s. 451.

[2] Helmholtz, Optique Physiologique, trans. by Javal and Klein, 1867, p. 70. Donders. On the Anomalies of Accommodation and Refraction of the Eye, trans. by W. D. Moore, 1864, p. 38.

of curvature, the indices of refraction, etc., and the six cardinal points, the exact position of the latter in the human eye can be shown to be as follows:

The anterior principal focus 12.8326 mm. in front of the cornea, the posterior principal focus 22.6470 mm., the anterior principal point 2.1746 mm., the posterior principal point 2.5724 mm., the first nodal point 7.2420 mm., the second nodal point 7.6398 mm. behind the cornea. The distance between the anterior principal focus and the anterior principal point—that is, the anterior focal length being then 15.0072 mm. = 12.8326 + 2.1746, and the distance between the posterior principal focus and the posterior principal point—that is, the posterior focal length being 20.0746 mm. = 22.6470 — 2.5724, and the distance between the two principal points 0.3978 mm., and the nodal points 0.3978 mm. The two nodal points and two principal points separated by only a distance of 0.39 mm. (about the $\frac{1}{83}$ of an inch) may be regarded practically as coinciding, and we may assume, therefore, for the sake of simplicity, without introducing any very sensible error in the construction, that there is but one principal point lying in the aqueous humor, 2.34 mm. behind the anterior surface of the cornea, and one nodal point lying in the back part of the lens, 0.47 mm. in front of the posterior surface of the lens, and, therefore, but one refractive surface, separating air on one side and water on the other.

FIG. 448.



Schema of reduced eye of Listing.

The eye so simplified, and constituting the so-called reduced eye of Listing, enables us to determine very readily the position and size of the inverted image of an external object formed upon the retina. Thus, let A B represent an object, an illuminated arrow, for example, placed vertically in front of the eye, then A d, B c, being rays of direction, will pass unrefracted through the nodal point K, while the rays from A that are refracted will come to a focus at d, and those from B to a focus at c, intermediate rays at some intermediate point (G). The rays of light taking this course through

the media of the eye, the inverted image of the external object will be found on the retina at D C. Further, since in simple lenses the size of the image is to the size of the object as the distance of the image from the lens is to the distance of the object from the lens, or, as in the case of the crystalline lens which we are now considering, as the distance of the image from the nodal point n k is to the distance of the object from the nodal point M k, it follows that the size of the image

$$= \frac{\text{size of the object} \times \text{distance of image from nodal point}}{\text{distance of object from nodal point.}}.$$

The distance of the image from the nodal point being, however, the posterior focal distance may be regarded as equal to the distance of the retina from the cornea (P'), minus the distance of the nodal point from the cornea (R), the distance of the object from the nodal point being equal to the distance of the object from the cornea (P), plus the distance of the cornea from the nodal point (R). Such being the case, and further calling the size of the image I and that of the object O, the formula for the size of the image may be conveniently expressed as follows :

$$I = \frac{O \times P' - R}{P + R}.$$

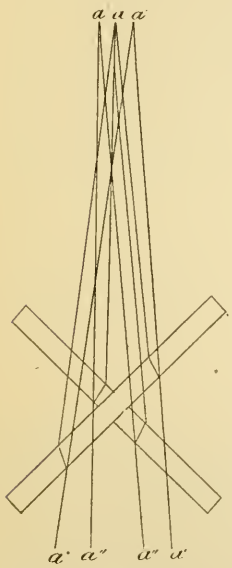
Supposing that the object O be 1000 mm. high, $P' = 22.6470$ mm., $R = 7.4$ mm., $P = 15.2396$ meters, then

$$I = \frac{1000 \times 15.247}{15.2396 + 7.4}.$$

That is to say, that the image of an object 1000 mm. (39.3 in.) in height seen at a distance of 15.2396 meters (50 feet) is 1 mm. ($\frac{1}{25}$ of an inch) in height, or a thousand times smaller. It will be observed also from Fig. 448 that the visual angle A k B—that is, the angle under which A B is seen—being the same as the angle under which the objects x y, r s, are seen, that the image of all three objects formed on the retina must be the same, and that, therefore, the apparent size of all three objects, though differing in size, will be the same. It is also obvious that the size of the visual angle depends on the size of the object and distance of the latter from the eye. From the fact of the smaller the visual angle under which distinct vision is possible the more acute the vision, the latter is evidently inversely as the size of the visual angle. The measure of the acuteness of vision in general use among physiologists, based upon this principle is a series of letters, C G B, the thickness of which is one-fifth of their height, and made of such a size that at a distance of twenty feet they subtend an angle of 5 minutes, the acuteness of vision being expressed by the ratio of the distance at which such letters are still distinctly recognized to the distance D, at which they subtend an angle of 5 minutes—that is

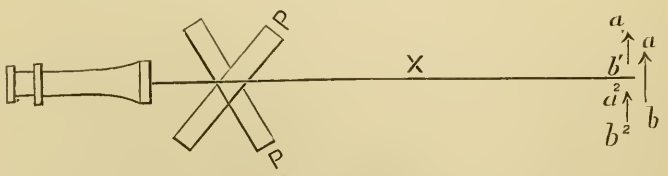
to say $V = \frac{d}{D}$. Suppose, for example, that the person whose vision is being tested can recognize a letter at ten feet, then his acuteness of vision will be $V = \frac{d}{D} = \frac{10}{20} = \frac{1}{2}$, that of one whose vision is perfect—that is in whom $V = \frac{d}{D} = \frac{20}{20} = 1$. Practically, the smallest visual angle permitting distinct vision is about 60 seconds, and, corresponding, as it does, to a retinal image of about $\frac{1}{250}$ of a millimeter ($\frac{1}{6250}$ of an inch), it will just about cover one of the cones of the retina. Two points seen under such a small visual angle would, therefore, appear as one. It has already been mentioned that the cardinal points, by means of which we follow the rays of light as they pass through the media of the eye and determine the position and size of the retinal image, are deduced from the indices of refraction of the aqueous and vitreous humors, lens, radius of curvature of cornea, etc., experimentally determined. Inasmuch as the methods by which the indices of refraction of the media of the eye are determined are essentially the same as in the case of water or glass, it need not in this connection be described again. The radius of curvature of the cornea and crystalline, however, being deduced by formulæ from the size of their reflected images, and the latter being measured by the ophthalmometer, this instrument merits at least a brief description. The principle upon which the ophthalmometer, invented by Helmholtz,[1] is constructed is, that if an image of an object a be viewed through two plano-parallel glass plates (Fig. 449) the image, through refraction, will apper double, a' a'', and that if the plates be so approximated that the inner edges of the two images are

Fig. 449.



Object viewed through two glass plates.

Fig. 450.



Schema of ophthalmometer.

brought in contact, then the distance between the outer edges of the two images will be twice the size of the single image. To

[1] Op. cit., p. 11.

measure the size of an image $a\ b$ (Fig. 450) by the ophthalmometer it is only necessary, then, to determine the lateral displacement of the images $a'\ b'\ a^2\ b^2$, which is accomplished by observing the angle made by the glass plates P P, with the axis X of the telescope, through which the image is viewed.

The size of the corneal image having been determined by means of the ophthalmometer, the radius of curvature of the cornea can be readily deduced from a well-known formula and was found by the author and Dr. Brubaker to be on the average in the horizontal meridian 7.797 millimeters and in the vertical meridian 7.552 millimeters, fifty persons being examined.[1] It may be mentioned in this connection that the radius of curvature of the lens is also determined by the ophthalmometer, though in a slightly modified manner. While it is true that rays of light falling

FIG. 451.

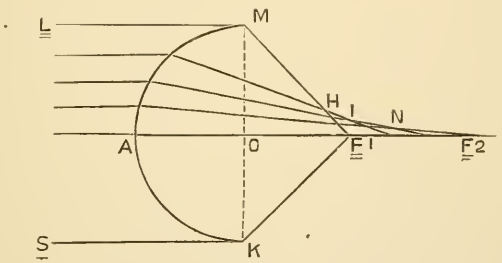


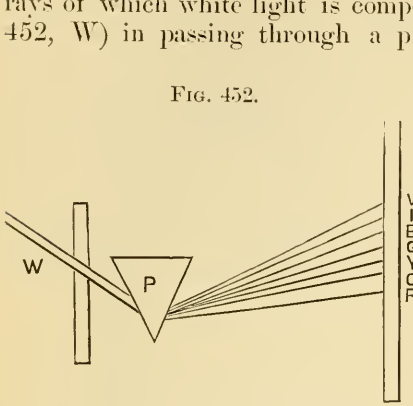
Diagram illustrating spherical aberration. (McKENDRICK.)

upon a refracting surface are brought to a focus in essentially the manner we have described in treating of such surfaces, it must be mentioned in this connection that of rays impinging upon a refractive surface, the peripheral ones being more refracted than the central ones are not brought to exactly the same focus as that of the latter, there being, in fact, many foci, and the image of the object consequently blurred and ill-defined. This condition, known as the aberration of sphericity (Fig. 451), and corrected in the making of lenses for microscopes, etc., by appropriate means, obtains also in the eye, though not to any marked extent, on account of the following circumstances: 1st, that the lateral most refracted rays are cut off by the iris, the latter acting precisely like the diaphragm of optical instruments; 2d, that the curvature of the cornea being ellipsoidal the lateral rays are less deviated than if the curvature was spherical; 3d, that the anterior and posterior surfaces of the crystalline lens are so disposed that the one corrects, to a certain

[1] For a detailed account of the construction of the ophthalmometer, method of using it and results obtained by it, see "Measurement of Radius of Cornea," by H. C. Chapman and A. P. Brubaker, Proc. Acad. Nat. Sciences, 1893, p. 349. Also, "History and Principles of Keratometry," by C. Weiland, Archives of Ophthalmology, Vol. xxii., 1893.

extent, the action of the other; 4th, from the fact that the refractive power of the lens, diminishing from the center to the circumference, the lateral rays are but little refracted. Inasmuch as a refracting medium does not act equally upon the different colored rays of which white light is composed, a ray of white light (Fig. 452, W) in passing through a prism (P) is not only bent, but decomposed into the colors of the spectrum, the condition so produced, that of chromatic aberration, giving rise to the formation of a colored image, white at the center, but surrounded at the borders by a circle of colors, like those of the rainbow. In the construction of optical instruments the chromatic aberration, or aberration of refrangibility, is corrected by combining lenses having a different dispersive power, as when a convex lens of crown glass is combined with a concave lens of flint glass, so, in the case of the eye, the chromatic aberration is, to a considerable extent, corrected through the crystalline lens, being composed of various layers of different consistence and of different refractive power. As a general rule, indeed, we are unaware that our eyes are not achromatic, like the lenses of microscopes and telescopes, but, under certain circumstances, our attention is very forcibly called to the fact. Thus, if, after looking at the cross hairs of an astronomical glass by a red light, we try to see them with another colored light, violet, for example, the eye must be changed, the eye, when adapted to see by a red light, not being able to see by the violet. Again, if we look at a candle-flame through cobalt blue glass, which transmits only the red and blue rays, the flame may appear blue, surrounded by violet, or *vice versâ*, according as the eye has been accommodated for different distances. It may be also mentioned that red surfaces always appear nearer than violet ones, since the eye, having to be accommodated more for the red than for the violet one, imagines the former surfaces to be nearer than the latter. In addition to the aberration of sphericity and of refrangibility, more or less present in the eye, from the fact of the focal length of the vertical meridian of the cornea being shorter than the horizontal meridian rays of light emanating from a point, do not converge to one. The condition so caused, and constituting astigmatism, is a defect from which few eyes, if any, are free. That the eyes are astigmatic one can readily convince himself by simply looking (Fig. 453) at two threads crossing each other at right angles in the same plane, or at two lines drawn in ink on a sheet of white paper

Fig. 452.



Decomposition of white light by prism.

disposed in a similar manner, when it will be observed at the point of distinct vision that it is impossible to see both threads, or lines, with equal distinctness at the same time; that to see the horizontal line distinctly, for example, the paper must be brought near the eye, and removed from it, to see the vertical line.

FIG. 453.

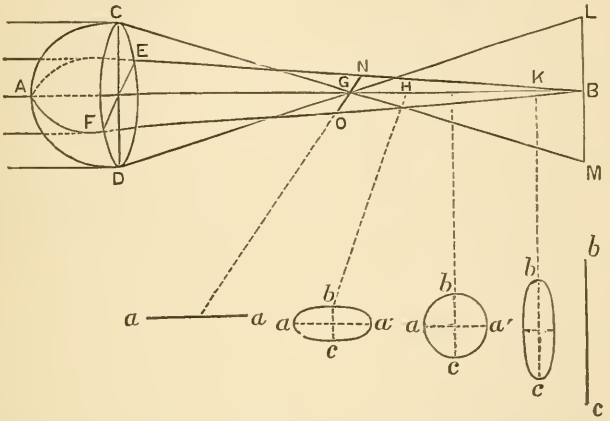
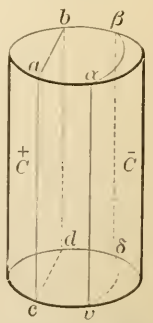


Diagram illustrating astigmatism. Lower figures illustrate appearance of rays, eye being at G H I, respectively. (McKENDRICK.)

While the detailed consideration of the subject of astigmatism belongs rather to the ophthalmologist than physiologist, it may be incidentally mentioned that the astigmatism of the cornea is, to a certain extent, naturally corrected by that of the lens, since the focal length of the vertical meridian of the latter differs from that of the horizontal, but in the reverse sense from that of the cornea.

FIG. 454.



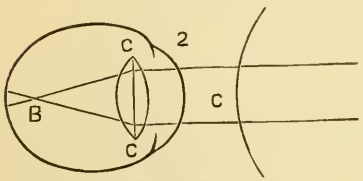
Cylindrical glasses for astigmatism. The section $C\,a\,b\,c\,d$ of the cylindrical lens (Fig. 454) represents a plano-convex, the section $C\,\alpha\,\beta\,\gamma\,\delta$, a concavo-convex lens. (LANDOIS.)

Astigmatism can be corrected by the use of a cylindrical glass (that is a lens so cut as to be without curvature in one direction), the curvature of which is such that if added to that of the horizontal meridian will make its focal length equal to that of the vertical one. The defects of the eye due to aberration of sphericity and refrangibility, or astigmatism, are so slight, usually, as not to attract attention; near-sightedness and far-sightedness are, however, unfortunately so common, and interfere to such an extent with vision, as to necessitate the wearing of glasses. The cause of myopia and hypermetropia, and their treatment constituting, like astigmatism, one of the most important subjects of ophthalmology, do not demand in this connection special consideration. As still further illustrating, however, the manner in which the rays

of light are brought to a focus in the eye, and serving in a measure also to elucidate the manner in which the eye is accommodated for different distances, a brief description of these abnormal conditions does not appear superfluous. Let us suppose, for example, that either through elongation of the whole eye or through the converging power of the lens being too great, that parallel rays of light are brought to a focus, not on the retina, but in front of it, at B (Fig. 455), circles of diffusion being formed, the image will be indistinct, blurred.

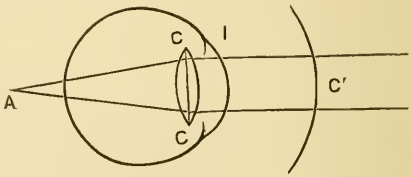
Obviously, in order to see distinctly under such circumstances, the object must be brought closer to the eye, so that the rays of light may be brought to a focus on the retina, hence the eye is said to be short-sighted or myopic. Such a condition can be, however, remedied by placing a suitable concave glass (C) in front of the myopic eye. The rays of light will then be diverged to such an extent that they will come to a focus upon the retina.

Fig. 455.



Myopic eye.

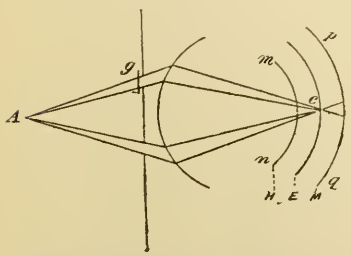
Fig. 456.



Hypermetropic eye.

On the other hand, let us suppose that, owing to the whole eye being too short or through the converging power of the lens being too small, parallel rays of light come to a focus behind the retina (Fig. 456 *A*), circles of diffusion being formed the image will be blurred and indistinct. In order to see distinctly with such an eye the so-called hypermetropic or far-sighted eye, parallel rays of light must converge sufficiently to come to a focus upon the retina. Inasmuch, however, as convergent rays of light do not exist in nature, the defect can only be remedied in such an eye, the latter being passive, by placing in front of the eye a suitable convex glass by which the parallel rays will be converged sufficiently to come to a focus on the retina.[1] A very ready and ingenious method for determining whether an eye is emmetropic—that is, normal, my-

Fig. 457.



Scheiner's experiment with Thomson's modification. *A*. Source of light. *E*. Position of retina in regard to the focus *c* of the rays entering through two apertures in a card, one of which is covered with a colored glass *g* in an emmetropic eye. *H*. Position of the retina *m n* in a hypermetropic eye. *M*. Position of retina *p q* in a myopic eye.

[1] In explaining to an audience the manner in which astigmatism, myopia, and hypermetropia, circles of diffusion, etc., are produced the author has found the artificial eye of Kuhne a very useful adjunct.

opic, or hypermetropic consists in placing a piece of colored glass *g*, red, for example, over one of the openings in the card used in Scheiner's experiment, as represented in Fig. 457. Supposing the eye to be emmetropic, it is evident that the colored red ray and white ray falling upon the retina at the same spot, but one image, a red one, will be observed. If the eye be myopic, however—that is, the retina is too far back, then through the crossing of the rays of light two images will be seen, a red one below and a white one above. On the other hand, if the eye be hypermetropic the two images will be seen, but the red one will be above, the white one below.

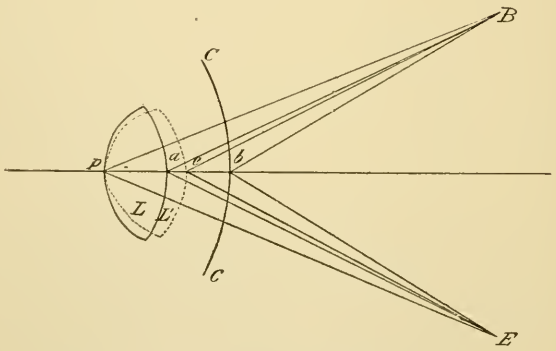
Accommodation.

In considering the manner in which the rays of light are refracted as they pass through the media of the eye, and the image of an external object formed upon the retina, we have supposed heretofore that both the eye and the object were at rest. Every one is familiar with the fact, however, that, notwithstanding that an object may approach or recede from the eye, in either case, at least within certain limits, it is as clearly seen in the first, as in the second position. Such being the case, evidently then the eye must undergo some change, otherwise, as the object approached the eye, the image would recede from the retina, being formed behind it, and as the object receded from the eye the image would recede from the retina in the opposite direction, being formed in front of it. Thus, let us suppose that the object being at *A B* (Fig. 448), and its image at *d c*, that the object is moved to *H*, its focus would then be formed behind the retina at *H'*, and the condition of the eye would be hypermetropic, as in the case of Scheiner's experiments just described, unless simultaneously with the movement of the object toward the eye some change was induced in the latter, by which the focus was kept upon the retina at *d c*. On the other hand, if the object be moved to *M*, then the focus would be formed in front of the retina, as at *M'*, and the condition of the eye would be myopic, unless simultaneously with the movement of the object from the eye, by some change in the latter, the focus was kept upon the retina at *d c*. The change undergone by the eye, and by which the image of the object is kept upon the retina, whether the object approaches or recedes, is known as the power of accommodation, and is without doubt due to a change in the shape of the lens ; the latter becoming more convex as the object approaches the eye, less so as the object recedes from it. As the object approaches the eye, the image tends to recede behind the retina, toward *H'*, but as the lens becomes more convex at the same time, the image tends to advance equally in front of the retina toward *M'*, the result of the antagonizing influences being such that the image neither recedes nor advances, but remains upon the retina. On the other hand, as the object recedes from the eye, the image tends to advance in front of

the retina, toward M', but as the lens becomes less convex at the same time, the image tends to recede behind the retina, toward H'; the image consequently remains as before upon the retina.

Before considering the means by which this change in the shape of the lens is effected, and through which the eye accommodates itself to different distances, let us first show how it can be experimentally demonstrated that such a change in the shape of the lens as that just described does actually occur during accommodation. With that object let the person whose eye is to be examined be requested to look at some distant object, and while so doing let the light from the flame of a candle (B, Fig. 458) fall upon the eye ($C'C$) at about the angle represented in the figure; if the eye of the observer be situated at E three images will be seen (Fig. 459); the first (b) an erect virtual image, due to the reflection of the light from the cornea (b, Fig. 458) to the eye of the observer at E; the

FIG. 458.



Change in the form of the lens during accommodation.

second (a) also a virtual erect image due to the reflection of the light from the anterior convex surface of the crystalline lens (a); the third (c); a real reversed image due to the reflection of the light from the posterior concave surface of the crystalline lens formed in the manner represented in Fig. 460.

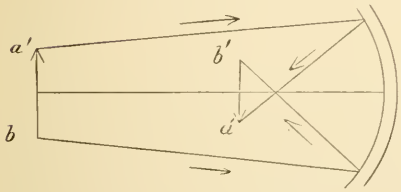
The three images being observed, let now the individual whose eye is being examined look at a near object, and at once the observer at E will notice that, while the position of the images (Fig. 459) a and c due to the reflection of the light of the candle B from the cornea and posterior surface of the lens remains unchanged, that of the image b due to the reflection of the light from the anterior surface of the lens is very much changed, it being now much closer to a, and also that it is smaller than when the individual whose eye is being observed looked at a distant object, which can only be accounted for on the supposition that the anterior surface of the lens increases in convexity, the light falling upon c instead of a

(Fig. 458), and which is the case for the radius of curvature of the anterior surface of the lens when the eye is accommodated for far objects, being 10 mm., but for near ones 6 mm. In performing this experiment the phakoscope of Helmholtz will be found a useful instrument. It consists (Fig. 461) essentially of a black trian-

Fig. 459.

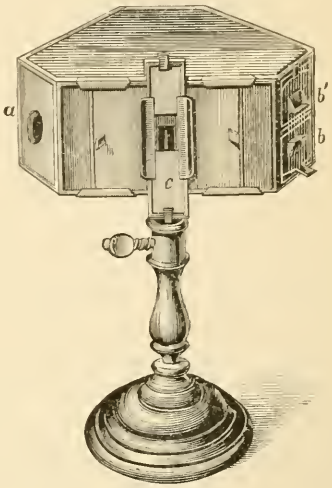
Reflected images in the eye.

Fig. 460.



Real reversed image of concave mirror.

Fig. 461.



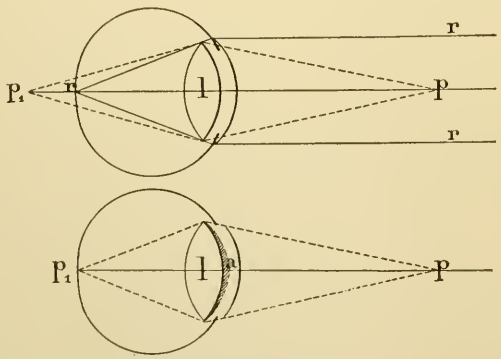
Phakoscope of Helmholtz. (McKendrick.)

gular box with four openings: the first opening in the base of the triangle supports a needle point, which constitutes the near object; the second opening, directly opposite to the first, receives the eye to be observed; while of the two remaining lateral openings, one containing prisms transmits the light, the other receives the eye of the observer. In using the phakoscope the individual looks first through the window at a distant object, and then at the middle point. It having been shown, then, that the lens becomes more convex—accommodates itself to see near objects—it only remains now to account for this change in the shape of the anterior surface of the lens. It will be remembered, in speaking of the action of the ciliary muscle, it was mentioned that, owing to its disposition with reference to the sclerotic and choroid, that in contracting it would draw the choroid forward, thereby relaxing the suspensory ligament of the lens, the effect of which would be that the lens, owing to its elasticity, would change its shape.

It would appear, therefore, that the change in the convexity of the lens, through which the eye accommodates itself to see near objects, is brought about by the contraction of the ciliary muscle. If such be the case, of which there can be but little doubt, the sense of effort which we experience in looking at near objects must arise from the contraction of the ciliary muscle. Accommodation can

only take place within a certain range, marked variation being observed however in this respect according to individual peculiarities. As a rule, objects situated at a distance of 62 meters (200 feet) and beyond to infinity, that is, at the punctum remotum or far point, to be seen, do not necessitate accommodation, as the rays of light, coming from such a distance, being parallel, come to a focus upon the retina; the nearer, however, the object approaches within this limit the eye, the more accommodating power is exercised, until a point is reached about 12.5 cm. (5 inches) from the eye, the punctum proximum or near point, which if exceeded by the object, cannot be compensated by any further change in the shape of the lens. The accommodation being then strained to its uttermost if the object comes still nearer the eye, the rays of light will not be focussed upon the retina. The range of accommodation of the eye for distance lies then between these two limits, that of the punctum remotum and punctum proximum. The power of accommodation of the eye can be measured by the converging power of a lens, which gives distinct vision of an object placed at the punctum proximum without necessitating any accommodation in the eye—that is, of a lens which brings the diverging rays of light from the punctum proximum to a focus on the retina, just as if they had come parallel from the punctum remotum, for which accommodation is not required in the normal eye. Indeed, that is exactly the effect of the change in the shape of the crystalline lens in accommodation, viz., that of retaining on the retina (Fig. 462, r), the focus of the rays of light diverging from the near point p, just as if they came parallel from the far point r r.

FIG. 462.

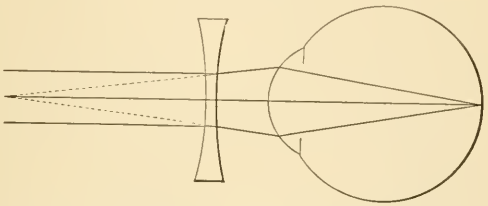


Condition of lens in the normal *passive* eye and during *accommodation*.

As the elasticity of the lens diminishes as a result of age and as further it becomes more flattened, the lens gradually loses the power of changing its shape, of becoming more convex as an object approaches the eye, and consequently the punctum proximum recedes further and further from the latter. The diminution in the range

of accommodation so produced is known as presbyopia, which, it will be observed, is an anomaly of accommodation, differing therefore from myopia and hypermetropia, which are anomalies of refraction. While the treatment of presbyopia belongs rather to the ophthalmologist than to the physiologist, it may be mentioned that it can be corrected by placing a lens before the eye, such as would give the rays the direction they would have if they came from the normal punctum proximum.

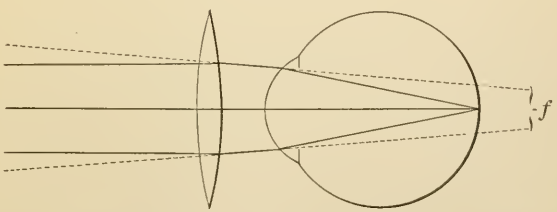
FIG. 463.



Action of a concave lens in front of the eye, causing parallel rays to enter the eye as if proceeding from a finite point in front of the eye. (BERRY.)

It may be mentioned also in this connection as regards accommodation that the myopic differs from the emmetropic eye in that the punctum remotum, or far point, is that point from which divergent rays of light come to a focus on the retina, the eye being passive (Fig. 463). While the far point in the myopic eye may be situated at a distance varying from 150 to 300 centimeters (60–120 inches) the punctum proximum, or near point, may be only 10 to 5 centimeters (4 to 2 inches) from the eye, the range of accommodation in the myopic eye is therefore limited. On the other hand, in the hypermetropic eye there is no punctum remotum, or far point, since neither divergent nor parallel rays come to a focus in such an eye when non-accommodated or passive. Inasmuch, however, as convergent rays falling upon the eye and directed, say to a point *f* (Fig. 464), will come to a focus on the retina, when still

FIG. 464.



Action of a convex lens placed in front of the eye, causing parallel rays to enter the eye, as if directed to a point at a finite distance behind the eye. (BERRY.)

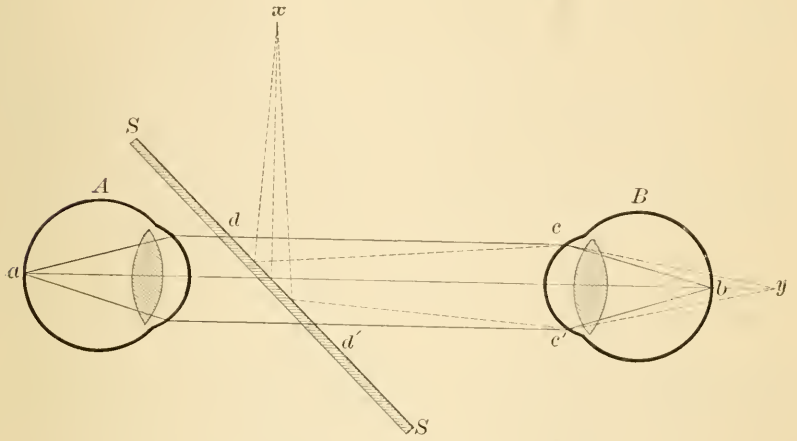
further refracted by passing through the cornea and crystalline lens that point is often said to be the punctum remotum, or far point, and negative, the converging rays being directed to that point

in the same sense as the diverging rays of the myopic eye are directed to or appear to come from the punctum remotum, or far point (Fig. 463), which in that case is positive. The punctum proximum, or near point, in the hypermetropic eye varies from 20 to 200 cent. (8 to 80 inches). The range of accommodation is, therefore, infinitely great. The ciliary muscle, by the contraction of which accommodation is accomplished, is innervated by nerve fibers that arise, as already mentioned, in the anterior part of the nucleus of the third nerve and pass thence to the eye by the ciliary ganglion and short ciliary nerves. That such is the case is shown by the fact that stimulation of this center is followed by contraction and the accommodation of the eye to near objects. Accommodation appears to be a voluntary act in response to visual sensations; at least we are led to accommodate simply by the desire to see distinctly near or far objects. In passing from accommodation for a near object to that for a far one it can hardly be said that we accommodate actively since the action is due simply to the relaxation of the ciliary muscle to the return to a condition more or less of equilibrium. In this respect the ciliary muscle differs from the iris, the muscle fibers of the latter being influenced, as we have seen, by two sets of nerve fibers, contractor and dilator. It should be mentioned, nevertheless, that atropin not only paralyzes the accommodation, rendering the eye hypermetropic, but dilates the pupil and that physostigmin renders the eye myopic and contracts the pupil. We shall see presently that in the converging of the axis of the eyes for the purpose of viewing near objects as in the accommodating of the eye for the same purpose the pupil contracts, just as we have seen is the case when the eye is exposed to light. This is an instance of what is called an "associated movement," and appears to be due to the fact that the will center, accommodating center, and pupil constrictor center are so intimately connected by nervous ties that when an impulse from the will center stimulates the accommodating center it stimulates at the same the pupil constrictor center. While in the case of most persons, in order to accommodate, the attention must be directed to some near or far object, it is said that by practice the aid of external objects may be dispensed with, and it is when this is accomplished that the pupil may appear to contract or dilate voluntarily, the effect being due to accommodation, as just explained.

The so-called Argyll Robertson pupil, frequently occurring in locomotor ataxia and progressive paralysis of the insane, is a further illustration of the intimate association existing between the voluntary accommodating and pupil constrictor centers. In this condition, while the pupil does not contract in response to light, a lesion existing in the nervous tie connecting the corpora quadrigemina and oculo-motor center, it does contract when the eye is accommodated for a near object, the centers causing contraction and accommodation being stimulated simultaneously by the will. In concluding the subjects of refraction and accommodation, it is

hoped that it will not be deemed superfluous if a brief account of the ophthalmoscope is offered by which the fundus of the normal and diseased eye is examined, and through which, in the hands of Donders, Graefe, and others, ophthalmic medicine was revolutionized.

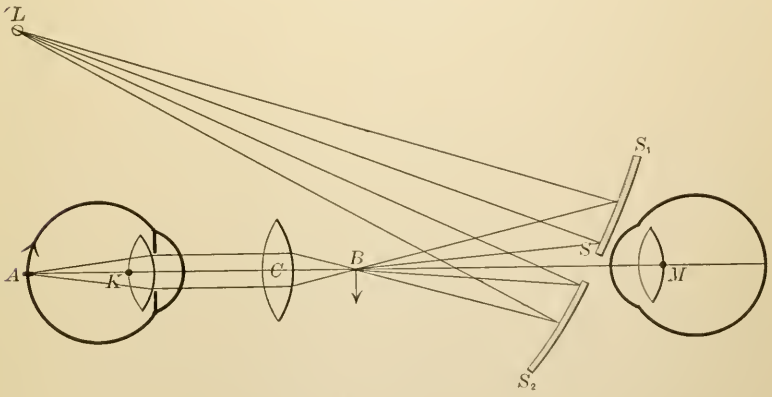
FIG. 465.



Arrangement for examining the eye of *B*. *A*, eye of observer. *x*, Source of light. *S*, *S*, plate of glass directed obliquely, reflecting light into *B*.

The interior of the eye under ordinary circumstances appears dark, since the observer being between the eye to be observed and the source of light intercepts the very rays whose reflection from the interior of the eye would form the image that it is desired to see. Further, the diverging rays from the interior of the eye, con-

FIG. 466.



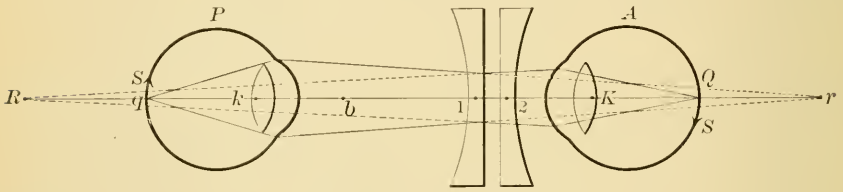
Ophthalmoscope with convex lens.

verging as they pass through its media, are brought to a conjugate focus outside of the eye, which, to be seen, would have to be viewed by the observing eye at a distance so far from the observed eye,

that little or nothing could be distinguished. If, however, the interior of the eye be illuminated by light reflected from an obliquely placed glass (Fig. 465), or a concave mirror, the center of which is perforated, and through and behind which the observer can view the eye, then the conjugate focus formed as just described by the rays reflected from the interior of the eye, can be more or less distinctly seen.

The image of the retina, entrance of the optic nerve, etc., as viewed by such a mirror as that just described, and constituting the original ophthalmoscope, become, however, much more distinct, if in addition to the mirror the observed eye be viewed through a lens. Suppose the lens used be a convex one (Fig. 466, *C*), then the rays of light from the retina *A* of the observed eye which would otherwise be brought to a focus rather near the observing eye

FIG. 467.



Ophthalmoscope with concave lens.

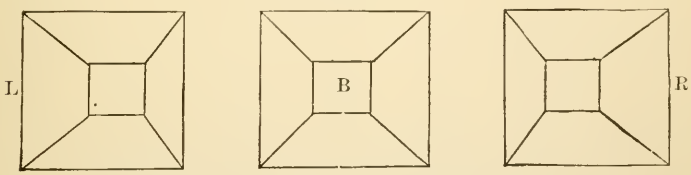
through the converging effect of the lens are brought to a focus at *B*, the image being real, inverted, and magnified. On the other hand, suppose that a concave lens be used, then the rays emanating from *Sq* (Fig. 467), which would come to a focus at *r* were it not for the lens, on account of being diverged by the latter, are projected back to *R*, the image being virtual, erect, and more magnified than when a convex glass is used.

CHAPTER XL.

BINOCULAR VISION. SENSATION AND PERCEPTION OF SIGHT. PROTECTIVE APPENDAGES OF THE EYE.

In describing the manner in which vision is effected we have hitherto supposed it as being accomplished by a single eye; it remains for us now to consider how both eyes act in viewing objects, or binocular vision. It might be naturally supposed from seeing an object single, when viewed with one eye, that it would appear double when viewed with both eyes. A little observation will, however, make it clear that with one eye we see but one side, so to speak, of an object, the right side, for example, with the right eye, the left side with the left eye, and that in order to obtain a perception of the entire object we must see the two sides of the object simultaneously. Thus, for example, when we look at a truncated pyramid (Fig. 468, B) placed in the middle line before us, the

FIG. 468.



Illustrating the principle of the stereoscope and binocular vision.

image falling upon the right eye is such as represented at R, that upon the left eye at L, the perception of the form of B being only obtained when the object is viewed by both eyes simultaneously. When two dissimilar images, one of the one eye, and the other of the other, are thus fused into one perception, the inference by the mind is that the object giving rise to the images is solid. Such, indeed, is the principle of the stereoscope, in which two slightly dissimilar pictures, such as would correspond to the images of two objects as seen by each eye respectively, are by means of mirrors or prisms cast upon the retina so as to give rise to a single perception, that of solidity, or of three dimensions, though each picture has a surface of but two dimensions. In order, however, that the two retinal images shall be fused into the one mental perception, it is essential that the two images shall fall on corresponding points of the retina, at *a a*, *c c* (Fig. 469), otherwise there will be double vision—hence, in viewing an object with both eyes the latter are converged, the angle made by the axes of the two eyes being large if the object is near, and small if the latter be distant.

As it can be shown, however, that the angles $a\ A\ a$ and $c\ C\ c$ are equal, it follows that the points $A\ C$ can not lie in a straight line, but in a circle, it being the property of a circle only, that triangles erected on the same chord and reaching the periphery have at the latter equal angles. The line joining the points $A\ C$ (Fig. 469), must, therefore, be a circle of which the chord is equal to the distance between the points of decussation ($K\ K$) of the rays of light in the eye. Such a circle is known as the "horopter," and all objects not lying in it are seen double, their images not falling upon corresponding points of the retina. Standing upright, and looking at the distant horizon, the "horopter" would be approximately for normal long-sighted persons, a plane drawn through the feet—that is to say, the ground on which they stand.

FIG. 469.

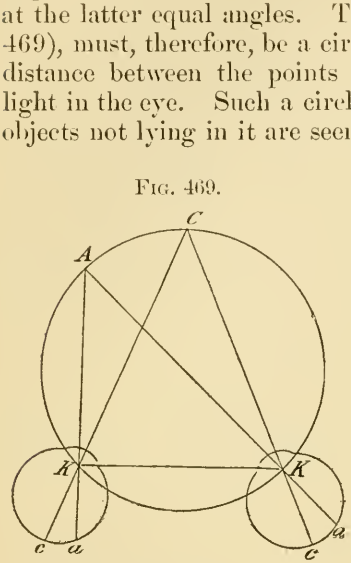


Diagram to illustrate the horopter. (McKENDRICK.)

The eyeball nearly filling the cavity of the orbit, and resting posteriorly upon a bed or cushion of adipose tissue, is moved by six muscles, the *recti* superior and inferior, externus and internus, and the obliqui superior and inferior. The effect of these muscles when acting separately is quite apparent from their origin and insertion. The four recti in the order named, arising from the apex of the orbit around the margin of the optic foramen, pass straight forward, piercing the capsule of Tenon or the fibrous membrane surrounding the sclerotic, to be inserted into the latter tunic at about the third or fourth of an inch behind the margin of the cornea, move the eye upward, downward, outward, and inward. The superior oblique muscle, arising from the optic foramen, proceeds toward the internal angle of the orbit and terminates in a round tendon, which, passing through a fibro-cartilaginous ring or pulley, is thence reflected backward and outward to be inserted into the sclerotic between the superior and external recti muscles. Its action is to rotate the eyeball downward and outward. The inferior oblique muscle arising from the orbital plate of the superior maxillary bone close to the external border of the lachrymal groove passes outward and backward between the inferior rectus and the floor of the orbit to be inserted into the external and posterior part of the sclerotic. Its action is to rotate the eyeball upward and outward. It can be shown, however, theoretically, as well as by actual observation, that the six muscles whose actions have just been described may be regarded as consisting of three pairs, each of which rotates the eye round a particular axis. Thus the recti superior and inferior rotate the eye up and down round a horizontal axis directed from the upper

end of the nose to the temple; the obliqui superior and inferior obliquely round a horizontal axis directed from the center of the eyeball to the occiput; the recti internus and externus from side to side round a vertical axis passing through the center of rotation of the eyeball situated a little behind the center of the optic axis, parallel to the median plane of the head, the latter being vertical. The different muscular actions just described may be briefly summarized as follows:

ACTION OF OCULAR MUSCLES.

Number of muscles acting.	Direction.	Muscles acting.
One	Inward,	Internal rectus.
	Outward,	External rectus.
Two	Upward,	Superior rectus.
		Inferior oblique.
	Downward,	Inferior rectus.
		Superior oblique.
Three	Inward and upward,	Internal rectus.
		Superior rectus.
		Inferior oblique.
	Inward and downward,	Internal rectus.
		Inferior rectus.
		Superior oblique.
	Outward and upward,	External rectus.
		Superior rectus.
		Inferior oblique.
	Outward and downward,	External rectus.
		Inferior rectus.
		Superior oblique.

The various movements of the eyeballs, as just described, conform to a general law, the so-called "Listing's law," which may be briefly described as follows: Let us suppose that the position of the eyeball is the primary one—that is, such in which the head is erect and vertical, and we look straight forward to a distant horizon, and that the visual axes, or the lines from the fixed point of vision to the center of rotation in the vitreous humor, 13.5 mm. from the anterior surface of the cornea, are parallel. Such being the case, it would appear that all movements of the eyeballs are around either a vertical axis from side to side, or a horizontal axis up and down, or an oblique axis, the latter situated in the same plane with the other two. In no case, however, does the eyeball rotate around the visual axis itself in a swivel-like movement—that is, such that the pupil would turn around like a wheel, since, if the eye were to so rotate, the rays of light would not fall upon corresponding points of the retina.[1] It may be also mentioned in this connection that while we can converge or make parallel the visual axes we cannot, at least without assistance of some kind, diverge

[1] It should be mentioned, however, that recent researches render it highly probable that the views generally prevailing as to the mechanism of the eye movements are not mathematically correct. See an interesting paper on that subject by Carl Weiland, Archives of Ophthalmology, Vol. xxvii., No. 1, 1898.

them, since, if we do so, the rays of light do not fall upon corresponding points of the retina.

It will be observed, from what has just been said of the action of the ocular muscles, that even in viewing an object with a single eye, that a considerable amount of muscular coördination must take place, since when the eye is moved in any other than the vertical or horizontal meridian three muscles at least must be stimulated, relatively to the amount of inclination of the visual axis needed. Such being the case in single vision, necessarily, then, the amount of muscular coördination required in binocular vision must be much greater. If the eyes of any person be observed, it will be noticed that the two eyes move alike, when the right eye moves to the right so does the left, and to the same extent if the object looked at be distant, if the right eye looks up so does the left, and so in every other direction. Briefly, then, the eyes move in such a manner that the images of an object always fall upon corresponding points of the retina, the essential condition, as we have seen, for the production of single vision, the movements of the two eyes ceasing to agree with each other only when the power of coördination is lost, through disease or by alcoholic or other poisoning.

It must be admitted, however, that the nervous mechanism, by which the coördination of the ocular muscles is accomplished, is as yet but imperfectly understood. That is to say, it has not been definitely shown exactly how the centers for the visual paths terminating in the occipital cortex and the centers from which arise the third, fourth, and six nerves are connected with the will center, supposed to be situated in the frontal lobe, in the front of the precentral fissure.

By movements of the eyes, apart from those of the head, the extent of the field of vision may amount to as much as 200 degrees in the horizontal and 200 degrees in the vertical meridian, that of a single eye being about 145 degrees for the horizontal and 100 degrees for the vertical meridian.

Sensation of Sight.

Regarding the sensation of sight as due to the stimulation of the retina by light, observation teaches, as might be supposed, that the intensity and duration of the sensation will vary according to the strength of the luminous vibrations and the length of time during which the latter continue to fall upon the retina. That the intensity of the sensation varies with that of the luminous object is a matter of daily experience, a wax candle, for example, appearing brighter than a rushlight. With a little experimentation it becomes soon apparent, however, that the ratio of the sensation to the stimulus is not a simple one, since while the sensations increase as the luminosity of the object increases, the sensations increase less and less, until finally there is no appreciable increase of sensation, however much the luminosity may be increased—that is to say,

when a light reaches a given brightness it appears so bright to us that we cannot tell when it becomes any brighter. It is much easier, therefore, to distinguish the difference between two feeble lights than the same difference between two bright lights—in fact, if the latter be very bright it becomes then impossible. Thus, for example, while there is no difficulty in distinguishing between the light of a candle and that of a rushlight, it would be impossible to distinguish such a difference between the light of two suns, supposing the light of the one to be in excess of that of the other in the same ratio as that of the candle over that of the rushlight, just as an addition of half an ounce to twenty pounds will not be appreciated by the sense of weight. Further, it will be found that if we let the shadows of two rushlights, for example, fall upon white paper, and then move one of the lights away until the shadow ceases to be visible, that in performing the same experiment with two wax candles the candle will have to be moved through the same distance as that of the rushlight before its shadow ceases to be seen, the smallest increment in light in both cases appreciable being invariable, about the $\frac{1}{100}$ of the total luminosity made use of. It is also evident that the duration of the sensation is longer than that of the stimulus, the sensation of sight and the stimulus of light being comparable, in this respect, to a muscular contraction, as induced by a single induction shock. It is for this reason that if two flashes of light follow each other sufficiently quickly, within the one-tenth of a second for a faint light, and the one-thirtieth of a second for a strong one, the two sensations arising are fused into one. Hence, the fact of a luminous point moving rapidly around in a circle giving rise to the sensation of a continuous circle of light, which reminds one of the production of muscular tetanus. That the duration of the stimulus of light necessary to give rise to the sensation of sight must be very short, is shown from the fact of the electric spark being seen, though the latter is known to last but the $\frac{1}{2500000}$ of a second. When a large portion of the retina is affected by light the total sensation experienced is greater in amount than when a small portion is so affected, a large piece of white paper, for example, affecting our consciousness more than a small piece. If, however, the surfaces of the papers be equally and uniformly illuminated, the small piece will appear as bright, or white, as the large one, the intensity being the same in both cases. Further, as might be expected, if the images of the two papers be situated upon the retina at sufficient distance apart, the two sensations will be distinct, the relative intensity of the same depending upon the brightness of the objects, while, if the images are so close to each other that the sensation fuses into one, then the total sensation experienced will be greater than that due to either one of the images, though not equal to the sum of the single sensations. As a general rule, the best eyes fail to distinguish two parallel white streaks when the distance separating them, as measured from the

middle of each, subtends an angle of less than 73 seconds, though some individuals can distinguish objects so close to each other that the distance separating them does not subtend an angle of more than 50 seconds. Now, as the retinal image corresponding to an angle of 73 seconds would measure in the schematic eye about 0.00536 mm., and that corresponding to an angle of 50 seconds, about 0.00365 mm., and as the average diameter of a retinal cone measures at its widest part about 0.004 mm., it is evident that the visual sensory area has a corresponding physical basis in the retinal anatomical area, which renders it highly probable that there is still another corresponding cerebral or perceptive area.

It has already been mentioned that, owing to the unequal refrangibility of different kinds of light, that white light in passing through a prism is not only refracted, but is decomposed into the seven kinds of light of which white light is composed, viz., violet, indigo, blue, green, yellow, orange, and red, or the colors of the spectrum. In considering, however, the manner in which we become conscious of the different colors of which the spectrum is composed, or of any colors or color, we must disabuse ourselves at once of the idea that what we call color exists outside of our own consciousness objectively as such, since what we call color in ourselves subjectively, can be shown experimentally to be due objectively to a vibration, an oscillatory movement, a wave of a definite length passing into the eye at a certain velocity, all kinds of light being so propagated. In fact, color objectively is to the eye what we shall see pitch in the case of sound is to the ear, the latter depending solely upon the number of vibrations striking the ear in a second. In other words, a wave of a certain length, propagated at a definite rate, in falling upon the retina, gives rise in us to a sensation of a particular color. Thus, the color red is due to the impinging upon the retina of a wave about $\frac{1}{1560}$ of a millimeter ($\frac{1}{39000}$ of an inch) in length, travelling at such a velocity that about 474,439,680,000,000 such waves enter the eye in a second; the color violet to a wave about $\frac{1}{2300}$ of a millimeter ($\frac{1}{57500}$ of an inch), about 690,000,000,000,000 such waves entering the eye in a second, the waves giving rise to the violet color being shorter than those to which the red color is due, but following each other into the eye more rapidly than the latter, the waves to which the other colors of the spectrum are due with reference to their length and velocity lying between the extremes just mentioned. The sensation of color depending then upon the successive impulses imparted to the fibers of the optic nerve by waves of different length travelling at different velocities, it is obvious that it would be useless to look into the external world for any attribute or quality that would correspond objectively to what we call in ourselves the sensation of color. In other words, the color red of an object is in ourselves, not in the object looking red, because the wave giving rise to red is reflected from the object into our eyes, the remaining waves being

absorbed by the object; similarly surrounding objects look red when viewed through a red glass, the wave giving rise to red being alone transmitted through the glass to our eye, the remaining waves being absorbed by the glass, and so with all other colors. Our knowledge of color depending then upon the impression made upon the sensorium by the waves of light is not absolute, but only relative. In other words, we do not know the light in itself—the thing itself, as Kant[1] expressed it—but only by just so much as the light or thing affects our consciousness. The extent to which sensation is dependent upon the susceptibility of the organism of being impressed by the external world, is shown by the fact that, notwithstanding the solar spectrum extends beyond the violet in one direction and beyond the red in another, the eye under ordinary circumstances is unconscious of the existence of these extremes, being so organized as not to be affected by the ultra violet or chemical rays, or the ultra red or heat rays. Our knowledge being due to sensations arising from impressions made by the environment upon the organism, cannot then be innate, but must have been ultimately derived from experience, and therefore relative, as held by Locke.[2] After what has just been said, it is evident that no physical or chemical changes in the retina will account for our sensation of color, since the cause of the latter lies not in the retina, which is simply an intermediate organ, correlating the physical with the psychical, but in that part of the cerebrum where the still physical vibration gives rise to sensation. Indeed, the cause of the sensation of color, as might be premised from the present imperfect state of physiological psychology, is not yet understood, although a great number of interesting observations have been made with reference to the effect of fusing colors, of complementary colors, of which a brief account at least in this connection must be given.

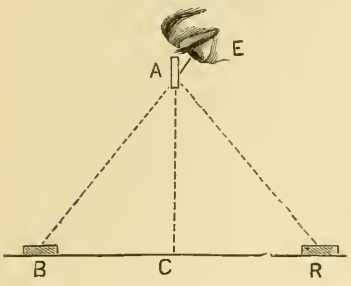
Though we have spoken of the solar spectrum consisting of seven colors, as a matter of fact, it is made up not only of such, but also of a great number of intermediate tints as well. External nature presents the same tints, and also a number of others like those of purple, brown, gray, etc., which, however, are not present in any part of the spectrum. While such tints are apparently due to distinct simple sensations, it can be shown experimentally that in reality they are compound ones, being obtainable by the fusion of two or more color sensations. Thus, purple, which, as just mentioned, is not present in the spectrum, may be readily produced by the fusion of red and blue, as, for example, by so placing a red and blue wafer and a glass (Fig. 470) that the light will be reflected from the red wafer (R) in the same direction as that coming from the blue wafer (B). In the same way the various tints of nature may be obtained by fusing different colors, sensations with that of

[1] Critique of Pure Reason, trans. by Max Müller. Second Part, p. 39. London, 1881.

[2] Of Human Understanding, Locke's Works, Chap. ii., Vol. i. London, 1883.

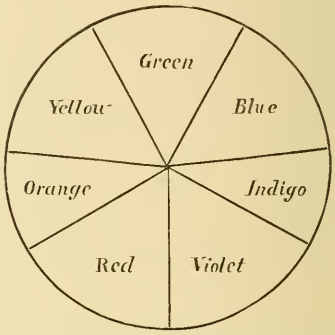
white or black, different kinds of brown resulting from mixtures of yellow, red, white and black, grays from white and black, as can be shown by making use of a rotating disk, on the surface of which colored sectors are painted, the resulting color being white, for example, in that of the instance represented in Fig. 471. Experi-

Fig. 470.



Lambert's method of studying combinations of colors.

Fig. 471.



Rotating disk of Sir Isaac Newton for mixing colors.

menting in this way, it can be shown that the quality of a color depends on the wave-length of its constituent waves and on the relative amount of colored and white light falling upon the retina in a given time, a color being saturated when unmixed with white light, as in the case of the colors of the spectrum.

As regards the fusion of colors, it is evident, from what has been said of the subject of color, that in mixing red and yellow to produce an orange, for example, undistinguishable from the orange of the spectrum, that the sensation of orange cannot be due to the uniting of the red and yellow waves differing in length from each other to form an orange wave differing in length from either, but that it is the mixture of the sensation of red and yellow that gives rise to the sensation of orange. In other words, the mixture is psychical, not physical. It is an interesting fact that certain colors, when mixed together in pairs in certain definite proportions, give rise to the sensation of white, as, for example, red and blue-green, orange and blue, yellow and indigo-blue, green-yellow and violet; such colors are said to be complementary colors, since given the color of one of the pairs, say red, all that is necessary or complementary to produce white is the other color of the pair, or green. It can be also experimentally shown, by means of the rotating disk, that the mixture in proper proportions of any three distinct colors of the spectrum arbitrarily selected, but sufficiently far apart, as, for example, red, green and violet, will produce white, and that by the further addition of white the sensations of all the other colors can be obtained. In order to avoid any misunderstanding as regards the production of the sensation of white, it should be men-

tioned that the mixture of red, green, and violet pigments, unless they are perfectly pure, will not produce white; a mixture of pigments being totally different from a mixture of sensations of colors, since the color produced by the mixing of pigments is due to the light which has escaped absorption by the same rather than the color due to a mixture of the colors. For example, the sensations of indigo and gamboge when mixed give rise to the sensation of white, the sensation due to a mixture, however, of indigo and gamboge pigments is green because the gamboge absorbs the blue, and the indigo absorbs the red and the yellow, while both reflect green. Facts like those just mentioned with reference to the fusion of colors, their complementary relation, the composition of white light, etc., led the celebrated Young,[1] in the beginning of the century, and Helmholtz,[2] in recent times, to advocate the view that all of our sensations of color are compounds of three primary color sensations, red, green, and violet, and that waves of different lengths give rise to all three of these sensations according to their particular length—that is to say (Fig. 472), the orange wave gives rise to

FIG. 472.

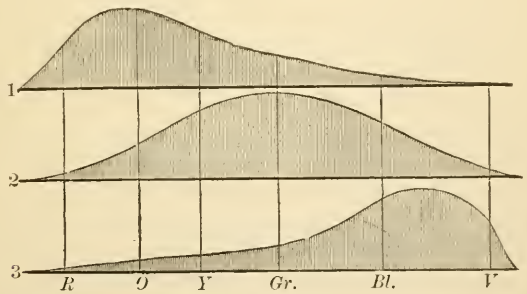


Diagram of three primary color sensations. 1 is the so-called "red," 2 "green," and 3 "violet" primary color sensation. *R*, *O*, *Y*, etc., represent the red, orange, yellow, etc., color of the spectrum, and the diagram shows, by the height of the curve in each case, to what extent the several primary color sensations are respectively excited by vibrations of different wave-lengths. (FOSTER.)

much of the first sensation, or red, less of the second, or green, and to little of the third, or violet; on the other hand, the blue wave gives rise to little of the red sensation, to more of the green, and to much of the violet, etc. The anatomical basis for the above is the assumption that three kinds of nerve fibers exist in the retina, the excitation of which gives rise respectively to the sensations of red, green, and violet—homogeneous light—all three of these so-called fundamental sensations, but with different intensities according to the length of the wave; long waves exciting most powerfully the fibers whose stimulation give rise to the sensation of red, medium waves those causing the sensation of green, short waves those causing the sensation of violet. Accepting provisionally the Young-Helmholtz theory of color sensation, it

[1] Lectures on Natural Philosophy. London, 1807. [2] Op. cit., p. 382.

serves to explain some of the phenomena of color-blindness, after-images, etc. While almost all individuals are able to appreciate differences of color, there are some, and the number is far greater than usually supposed, who are unaffected by certain colors, the most common defect being an insensibility to red, blindness to green and violet being rare. Thus, for example, in Daltonism, or blindness to red, so called on account of its having been observed in the celebrated Dalton, the red end of the spectrum appears dark, a red gown lying on a green grass plot, a red cherry among green leaves, are distinguished, not by their color, but by their form, the color of the gown or the fruit appearing to such an eye not red, but green like that of the grass or leaves. Remembering that green is the complementary color to red, and supposing that in a daltonic eye the fibers whose stimulation in an ordinary eye would give rise to the color of red are either absent, diseased, or paralyzed, the phenomenon just referred to can be accounted for. Similarly, if, after a red patch has been looked at steadily for some time until the eye becomes fatigued, a white surface be looked at, a green patch will be seen instead of the red one, the green fibers of the retina, so to speak, being fresh, are susceptible of being excited by the green color (or wave giving rise to it) of the white light reflected from the paper, the red fibers being, however, exhausted, are no longer susceptible of being excited by the red color (or the wave giving rise to it) of the white light. In the same manner many other negative after-images can be explained, so called as contrasted with positive after-images which are simply due to a sensation, being continued even after the object giving rise to it has been removed from the field of vision. Thus, for example, if the eye be directed momentarily to the sun the image of the latter will be present for some time after, or if a window be looked at for an instant on early waking, and the eye then closed, an image of the same with its bright panes and darker sashes will persist for some time. While the Young-Helmholtz theory of color sensation is accepted by many physiologists, another theory has been advanced by Aubert [1] and Hering [2] among others, the latter of whom maintain that the primary color sensations are white, black, red, yellow, green, and blue, and that these different sensations are due to the changes in the so-called visual substance of the visual apparatus, the changes giving rise to the sensations of black, green, and blue being processes of a constructive-assimilating kind, those giving rise to the sensations of white, red, and yellow, of a destructive-assimilating kind. If Hering's view be accepted, then black and white, green and red, blue and yellow, far from being complementary, must be regarded as antagonistic to each other, and the visual substance assumed to be always undergoing changes, never in a state of rest. The limits of this work will not permit of further illustration or discussion of

[1] Physiologie der Netzhaut, 1866.
[2] Wien. Sitzberich, lxvi. (1872), lviii., lxix., lxx.

the relative merits of the Helmholtz and Hering theories of the sensations of color; it may be pointed out, however, once more, that whether the one or the other theory be accepted, we are not a whit nearer the explanation of the sensation of color, since the transformation of the ultimate physical vibration or wave into the psychical color sensation takes place not in the retina but in the cerebrum.

Perception of Sight.

It has already been mentioned that as the apparent size of an object depends upon the visual angle, if two objects, though of different size, subtend with the eye equal angles—that is, if their visual angles are the same—the apparent size of the objects will be the same. The real size of an object is therefore not determined by the sense of sight, the latter only giving rise to the sensation of its apparent size. The estimate of the real size of an object is really an inference based upon its apparent size, but modified by the knowledge of its distance from the eye. In other words, it is not a simple sensation, but a judgment based upon the sensations of touch, as well as those of sight. Knowing the distance of an object from us, we infer from its apparent size its real size; and conversely, knowing the size of the object, we infer its distance. Thus, if the image of some well-known object, a man, for example, appear in our field of vision, and we know how far off the man is, we infer his size from that of our retinal image; and, conversely, knowing the size of the man, if his retinal image be very small, we infer that the man is very far off. That our estimate of the size of an object is dependent upon the knowledge of its distance from us, is shown from the fact that if we have no means of even approximately estimating the latter it is impossible to obtain any idea of its size. Thus the sun, though about four hundred times the distance of the moon, is apparently of the same size as the latter, but we infer from that very reason that the one body is larger than the other; did we not know, however, their relative distance from the earth it would be impossible to say which of the two, the sun or the moon, was the larger body. Our estimate of the distance of objects is not only based upon their size, but largely upon the presence of surrounding and intermediate objects, it being difficult to estimate the distance of an object entirely isolated, as in looking at a single distant object at sea. The muscular sensations arising through the contraction of the ocular muscles in converging the visual axis for near objects, and making them parallel for distant ones, aid us very much in forming a correct judgment as to the distance of objects. As with our estimate of the distance of objects, so with that of the idea of solidity, which is essentially an estimate of the distance of the different parts of an object, the idea being a judgment, a mental combination of the two dissimilar pictures formed upon the retina, the image of the object as viewed by the

right eye being, as already mentioned, different from that as viewed by the left eye, the resultant image being seen in relief, and giving rise to the idea of solidity. The fact that we see objects erect, though their images are reversed upon the retina, as already mentioned, is due to the fact of the sensation of the image derived from the sense of sight being modified by the sensation of the object derived from the sense of touch. The mind associating images situated at the upper and inner part of the retina with the objects giving rise to them but situated below and to the outer side of the eye, and images at the upper and outer part of the retina with objects situated below and to the inner side of the eye, and projecting outward, the images or the luminous sensation back to the object giving rise to them, finally perceives the objects erect. In the same way, but conversely, when a phosphene or luminous image is created by pressing, say on the outer or lower side of the eyeball, the image appears to lie above and to the inner side of the eye. Indeed, the association of the sense of sight with that of touch in obtaining the ideas of the size, distance, solidity, position of objects, etc., is so intimate that were our knowledge of the same derived through the sense of sight alone it would be of the most inexact and unreliable character. That such is the fact has been shown by cases like those of the youth reported by Cheselden,[1] who for some time after the sense of sight was given him, he having been born blind, saw everything flat, as in a picture, and supposed that objects when seen touched his eyes, as objects when felt touched his fingers. The newly acquired sense of sight at first rather hindered him in finding his way about the house, which he could do perfectly well by the sense of touch alone. The fact that the youth could not tell of his two pets which was the cat, and which was the dog, by the sense of sight alone, though he could at once distinguish them by feeling them, led him one day to feel the cat and at once look at her, and then setting her down, said, "So puss, I shall know you, another time." What has just been said renders it very probable, as held by Locke,[2] that a person born blind, on suddenly obtaining his sight, would be unable by sight alone to distinguish a cube from a sphere—that is, to be able to say which was the sphere, which the cube, for though he knows how the sphere or the cube affects his touch, he has not learned by experience, as yet, that if the cube, etc., affects his touch so and so, it will affect his sight so and so, and enable him by sight alone to distinguish it from the sphere. Since our perception of external objects is elaborated out of the sensations that the retinal images give rise to, it might be supposed that the perception would invariably correspond to the sensation, just as the latter would correspond to the retinal image causing it. As a matter of fact, however, such is not invariably the case, discrepancies arising between the retinal image and the perception, some of cerebral, others of retinal origin,

[1] Phil. Trans., 1728, p. 477. [2] Op. cit., Book II., chap. ix., p. 256.

the effect of which is so to modify the perception that the usually reliable judgment as to the size, distance, etc., of objects is perverted. Thus, for example, the white square (Fig. 473) on the black ground appears larger, and the black square on the white

Fig. 473.

Illustration of irradiation. (McKendrick.)

Fig. 474.

Illusions of size.

ground smaller, than it really is, the over-lapping of the white light in either case, or the irradiation, being due, as it were, to retinal or cerebral fibers other than those directly stimulated by the light being thrown into sympathetic vibration. If a white strip be placed between two black ones the inner edges of the former—that is, the edges nearest the black—will appear by contrast whiter than the median portions. In the same manner, the center of a white cross placed upon a black background will often appear shaded, as compared with the remaining parts. The judgment may also be at fault with reference to size, as in Fig. 474, when though the dis-

Fig. 475.

Zœllner's figure, showing an illusion of direction. (McKendrick.)

tance A B is equal to the distance B C, the former appears to be the greater; or with reference to direction, as in the case of Zœllner's (Fig. 475) lines, which, if looked at obliquely, will give

the impression that the vertical lines, though parallel, converge or diverge, and the oblique lines, though continuous across them, are not exactly opposed to each other. That the above effect is due to an error of judgment, is shown by the fact that by an effort it may be controlled, the lines being then seen as they really are. If two equal squares be marked, one with vertical, and the other with horizontal, alternate dark and light bands, the former will appear broader, and the latter higher than it really is. Short persons should therefore wear dresses horizontally striped if they wish to increase their apparent height, and stout persons avoid wearing longitudinally striped ones. Many other such examples might be given, but the above will suffice to illustrate the errors of judgment that the sense of sight alone may lead one into.

Protective Appendages, etc., of the Eye.

The eyeball, with its muscles, etc., is protected by the bony orbit, the outer wall of which is stronger than the inner one, the eye being more exposed to injury from the outer than the inner side ; the inner wall of the orbit projecting, however, considerably beyond the outer wall, the extent of vision is far greater in the outward than in the inner direction. The upper semi-circumference of the orbit and the superciliary ridge is provided with short, stiff hairs, the eyebrows, which serve to protect the eyelids from the perspiration of the forehead, and to shade the eye from excessive light. The eyelids consist of folds of very thin integument lined by mucous membrane, the conjunctiva, the subcutaneous connective tissue being thin, loose, and free from fat, and containing small papillæ, and sudoriferous glands. The eyelashes, the short, stiff, curved hairs projecting from the borders of the lids in two or more rows, serve to protect the eye from dust, and, to a certain extent, also, to shade it. The palpebral cartilages, extending from the edges of the lids, which they support, to the margin of the orbit, are small, elongated, semilunar plates, attached internally by the tendo-palpebrarum to the lachrymal groove, externally by the external tarsal ligament to the malar bone, and supported by the palpebral ligament. On the posterior surface of the tarsal cartilages, lying just beneath the conjunctiva, are found the Meibomian glands, which, in structure, are modified sebaceous glands, whose secretion, an oily fluid, in smearing the edges of the eyelids, prevents the overflow of the tears. The eyelids serve to protect the eyeball, their movements constituting, respectively, the opening and closing of the eye, the act of winking favoring the passage of tears over the globe and through the lachrymal canals into the nasal sac ; and hence, when the orbicularis palpebrarum is paralyzed, by the contraction of which muscle the eye is closed, the tears do not, as readily as usual, pass into the nose. The eye is principally opened by the raising of the upper eyelid through the contraction of the levator palpebrarum, though it is also opened through the elevation of the upper and depression

of the lower eyelids, respectively, through the action of the plain muscular fibers existing in both eyelids, and which are innervated by the sympathetic, the orbicularis palpebrarum being supplied, as has already been mentioned, by the facial and the levator palpebræ by the third nerve.

The eyes are usually kept open, almost involuntarily, though we can close or open them at will; the action of the orbicularis muscle is, however, to such an extent of a reflex character that if the globe of the eye be touched or irritated, or if the impression of light produces pain, it is then impossible to keep the eye open. It has already been mentioned that the inner surface of the upper and lower eyelids is lined by a mucous membrane, the conjunctiva. The conjunctiva, continuous with the membrane lining the puncta lachrymalis, and the lachrymal ducts, is reflected forward from the inner periphery of the lids over the eyeball, that lining the lids being called the palpebral, that covering the eyeball the ocular conjunctiva; the latter differing, further, in its sclerotic and corneal portions. At the point where the membrane is reflected upon the globe it presents a superior and inferior fold, the former containing numerous glandular follicles and minute lachrymal glands. At the inner canthus there is a vertical fold, the so-called plica semilunaris, which, morphologically, corresponds to the inner and third eyelid, or the nictitating membrane present in many of the lower animals, as in sharks, birds, and some mammals. The caruncula lachrymalis, the reddish, spongy elevation situated at the inner portion of the plica just mentioned, consists of a collection of follicular glands with a few delicate hairs on its surface. The eye is kept continually moist by a thin, watery fluid secreted by the lachrymal gland, which, after being spread over the globe by the movement of the lids and of the eyeball, passes into the lachrymal apparatus, any overflow upon the cheek, constituting the tears, being prevented ordinarily by the secreting of the Meibomian glands. The lachrymal gland, about the size of an almond, ovoid in form, and of a racemose type of structure, is situated at the upper and outer portion of the orbit. It presents six to eight ducts, five or six of which open above, and two or three below the outer canthus of the eye. The tears consist largely of water, which amounts to over 90 per cent., the remaining elements being made up of small quantities of epithelium, albumin, sodium chloride, alkaline and earthy phosphates, mucus, and fat. The actual amount of the lachrymal secretion has not been determined. Every one is familiar with the fact that the secretion of tears is very much increased by emotion; hypersecretion may be also readily induced through reflex action by irritation of the conjunctiva, nasal mucous membrane, muscular effort, laughing, coughing, and sneezing, the efferent nerves involved being the lachrymal and orbital branches of the fifth nerve, branches of the cervical sympathetic; the afferent nerves varying according to the exciting cause. The lachrymal apparatus, through which

the tears usually flow into the nose, begins by two little points or orifices, the puncta lachrymale of the eyelids, which leads into the upper and lower lachrymal canals, the latter surrounding the caruncula lachrymalis. Just beyond the caruncula the canals unite and pass then into the lachrymal sac or the upper dilated portion of the nasal duct. The duct being about half an inch in length, fibrous in structure, and lined with ciliated epithelium, empties into the inferior meatus of the nose. Reflux of the tears from the nose to the eye is prevented by the folds of mucous membrane, present in the lachrymal canals, and at the opening of the duct into the nose, acting as valves, the latter one being, in this respect, much more efficient than the former.

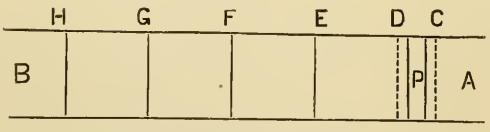
CHAPTER XLI.

PHYSIOLOGICAL ACOUSTICS.

JUST as we have seen that in order to understand how vision is accomplished, some knowledge of optics is absolutely essential, so for the comprehension of the manner in which the voice is produced and sound is heard, a knowledge of acoustics is equally indispensable. Similarly as in the case of vision, attention was continually being called to the distinction between the sensation of sight and the waves of light giving rise to it, so in case of sound the sensation of hearing must be distinguished from the waves of sound giving rise to it, for what constitutes in us subjectively hearing is out of us objectively vibration. Our knowledge of sound is then like that of light, etc., of all knowledge, only relative, depending upon the vibrations and the extent of the susceptibility of the auditory apparatus being impressed by the same. Let us consider first, then, how sound is produced in general, and more especially by the larynx, and then turn to the consideration of how it is appreciated by the brain, through the ear and auditory nerve. The sensation of sound, or more properly of musical sound as contrasted with mere noise, is due, as we shall see presently, to the periodic rhythmic vibratory wave-like oscillation of the sounding or sonorous body, being transmitted by an elastic medium, usually the air, to the ear, noise being due to the oscillations being transmitted in an unperiodic, irregular manner. The drawing of the bow across the strings of a violin gives rise in us to what we call music, the shaking of a box containing nails, chisels, files, etc., to noise, the auditory nerve being affected in the one case by oscillations following each other in a regular, orderly sequence, and in the other by irregular, disorderly oscillations following each other in no sequence at all. The effect of noise upon the ear has often been compared to that of flickering light upon the eye, the painful experience in both cases being due to the sudden, abrupt, and irregular stimulation of the auditory and optic nerves respectively. Nevertheless, the difference between noise and sound is not an absolute one, being rather one of degree than of kind, as shown by the noise due to the rattling of a carriage over stones, becoming a musical sound as soon as the oscillations become rhythmical and regular in character. Let us endeavor to explain now, by a few simple illustrations, what is meant by periodical rhythmical vibrations, to which the sensation of sound has just been said to be due. Let us suppose, for example, that a number of persons are standing in a row, one behind the other, each individual's hands resting against the back of the one in front of

him, and that the individual at the one end of the row be suddenly pushed from behind, forward against the individual standing in front of him, the latter in turn will be pushed against the individual standing in front of him, and so through the whole row until the last individual will be pushed forward. Further, let us suppose that the push be not very violent, and that the individual at the one end of the row first pushed forward regains his erect position, and then the second regains his, and so on through the whole row until the last man at the other end of the row regains his position, it is evident that though each individual person may have swayed to and fro, oscillated pendulum-like through a very small fractional part of the distance through which the push has passed, the push itself or the wave may have been transmitted through a long row of individuals, a hundred or more. Conceive the last individual body, the last individual of the row, to be the tympanic membrane of the ear, the intermediate individuals of the row, laminæ of air or of any other elastic medium, and we can readily picture to ourselves what is taking place in the air, as the wave giving rise to the sensation of sound passes from the sounding body to the ear. The conditions being strictly analogous in both cases, each lamina of air being pushed forward against its neighbor, through the elasticity of the air, after giving up its motion to the next lamina will recoil again, and just as in the case of the individuals in the row, the more rapid the to-and-fro motion of the laminæ of the air, the greater the velocity of the push transmitted through the row and of the sound wave through the air. On account of the importance of thoroughly understanding the manner in which the sound is propagated in air, let us consider a little more particularly the case in which it is propagated through a tube of indefinite length. Let A B (Fig. 476) be a tube filled with air, the temperature and pressure being

FIG. 476.



To illustrate propagation of sound in air.

constant, and let us suppose that P be a piston, oscillating rapidly from C to D, then as the piston passes from C to D, it condenses the air in the tube, the condensation, however, not extending at once throughout the whole tube, but on account of the great compressibility of the air only to the extent D E. As the piston, however, then passes from D back to C, the air in contact with its anterior face expands and becomes rarefied, and by the time that the piston reaches C the air has become rarefied to an extent (E D) exactly equal, but opposite in direction to that of the previous condensation (D E). Supposing the tube A B to be divided into equal parts

(D E, E F, F G, G H), etc., it is also evident that by the time the condensation beginning at say E reaches F, due to the forward movement of the piston from C D, condensing D E, that the rarefaction beginning at E due to the backward motion of the piston from D to C will reach D, and that the forward condensation E F and backward rarefaction E D are equal and opposite in direction. The condensed and rarefied laminæ of air (E F, E D), so produced during the forward and backward movements of the piston, constitute a wave, a vibration, an undulation, just as the to-and-fro motion of a pendulum constitutes a vibration, the length of the sonorous wave or vibration being the distance traversed by the sound during the complete vibration, or to-and-fro movement of the vibrating body causing it. In France, however, a vibration is considered as being either the to or fro movement, not both, that is to say, each English vibration is equal to two French ones. By a vibration we shall always mean the double vibration equal to two single French ones. That is to say, as the piston passes from C to D, the sound travels from D to E, and as the piston passes back from D to C, the sound passes on from E to F. It need hardly be added that the length of the undulations will be less in proportion to the rapidity with which they follow each other, and that though the to-and-fro movements of the individual particles of the air giving rise to the condensations and rarefactions may be very slight, and the undulations long or short, few or many in a given time, the sound wave itself may be transmitted to a great distance.

Such being the manner in which a sound wave is propagated in a cylindrical tube, there will be no difficulty in comprehending how sound waves are propagated in an uninclosed medium, if we only conceive each molecule of the vibrating body as acting as the piston in the tube, a series of waves alternately condensed and rarefied being then generated around each center of vibration, the sound radiating in all directions, like the waves of water spreading out upon the surface from some point of disturbance—the intensity of the same gradually, therefore, in both instances diminishing. That sounding bodies are actually vibrating can be readily demonstrated. In the case of strings it is a mere matter of observation, the vibrations being so apparent as to be visible to the naked eye. It will be remembered, also, that we made use of the traces due to the vibration of a reed or tuning fork to determine small intervals of time, and, indeed, by such graphic methods we are accustomed to test the accuracy of our standard tuning forks. Apart, also, from the thrill experienced when a sounding bell is touched, its vibrations are made visible indirectly at least by the brisk to-and-fro movement of pith balls placed in contact with it. The vibrations of a sounding glass plate can also be rendered visible, as first shown by the celebrated Chladni [1] by sprinkling sand upon its surface, the sand only remaining at rest upon the part of the plate not in vibra-

[1] Die Akustik, Leipzig, 1802, s. xvi.

tion, and disposing itself in characteristic lines according to the shape of the plate and the character of the sound. It has already been mentioned that the vibrations of sonorous bodies can only give rise to the sensation of sound in us by the intervention of an elastic medium interposed between the ear and the vibrating body, and vibrating with the latter. While this medium is usually the air, the waves of sound are also transmitted through gases, vaporous liquids, and solids. A diver at the bottom of the water can hear the sound of voices on the bank; the scratching of a pen at one end of a piece of wood is heard at the other end; while the earth conducts sound so well that if at night the ear be placed upon the ground the steps of horses or other sounds or noise can be heard at a great distance off. That the waves of sound are not propagated in vacuo, as first shown by Hawksbee,[1] can be very easily demonstrated by means of an apparatus which consists of an air-pump and receiver standing upon wadding, and a bell, the hammer of which is made to strike by clock-work set going by the raising of a detent passing through the top of the receiver. The bell, etc., having been placed within the receiver, the air from the latter exhausted by the pump, and the hammer made to strike, no appreciable sound will be heard until the air is allowed to pass into the receiver. By allowing hydrogen gas, which is fourteen times lighter than air, to pass into the receiver, and by which the air is rendered very much more attenuated, such a perfect vacuum is obtained that not the slightest sound is heard, even though the ear be placed against the bell itself. The experiment just described is not only a very striking one, as proving that sound is not transmitted in vacuo, or a very attenuated atmosphere, but it illustrates the difference between the cause of sound and the sensation of sound, since, though the hammer may be seen striking the bell and causing it to vibrate, no sound is heard as long as the vacuum is maintained, there being no intermediate medium to transmit the vibrations of the bell to the ear. Sounds, however produced, whether by strings, reeds, tuning forks, bells, plates, etc., are distinguished by their intensity, pitch, and quality, and as these differences in the character of sounds must be thoroughly appreciated in order to understand how the voice is produced, and sounds are heard, let us endeavor, therefore, to explain them now a little in detail.

Intensity of Sound.

By the intensity of sound is meant the loudness of sound. We hear one sound louder than others because the particles of air set in motion by the sounding body strike the tympanic membrane of the ear harder in the one case than another. Just as the force with which a ball strikes a target can be shown on mechanical principles to be proportional to its weight and the square of the velocity with which it is moving, so the force with which the air particles strike

[1] Phil. Trans., Vol. xxiv., p. 1004.

the tympanic membrane can be shown to be proportional to the square of the maximum velocity with which it is moving. The intensity of a sound depends, however, on the density of the air in which the sound is generated, and not on that of the air in which it is heard. Thus, while a cannon fired in a valley may be heard at the top of a high mountain above, the same cannon fired at the top of the mountain will not be heard in the valley below, the sound generated in the dense air of the valley being louder than that generated in the rare air on the top of the mountain. The intensity of the sound is also proportional to the square of the amplitude of the vibration, the amplitude being the width of swing, the distance through which the air particle moves to and fro when the sound wave passes it.

That such is the case can be readily shown by means of vibrating cords; for if the latter are long, the oscillations being visible to the eye, it will be seen that the sound becomes feebler in proportion as the amplitude of the oscillation decreases. The intensity of sound is modified by the distance of the sonorous body from the ear, varying inversely as the square of the distance; that is to say, for example, the intensity of the sound of a bell, situated at a distance of 20 yards from the ear, would be only one-fourth of the intensity of the same bell if situated at 10 yards from the ear, or half the distance; or what is the same thing, the intensity of four bells, situated at a distance of 20 yards, is the same as that of one bell situated at a distance of 10 yards from the ear, supposing, of course, that the bells are all of the same size, and other conditions equal. That the intensity of the sound must diminish in the above ratio—that is, as the square of the distance—will become evident when it is borne in mind that, as the spherical waves of sound radiate outward from the center of disturbance toward the periphery, the mass of air set in motion must be continually augmented as the squares of the distance from the center, the areas of circles being to each other as the squares of their radii. The matter affected increasing then as the square of the distance, the intensity of the sound must diminish in the same ratio. If, however, the wave of sound be propagated in a tube, lateral diffusion being prevented, as in Fig. 476, then the sound can be transmitted through great distances with very little diminution in intensity; thus Biot found that a person whispering at one end of one of the empty water-pipes of Paris, a tube 3,120 feet in length, could be heard at the other end, and that the firing of a pistol at one end of the tube put out a lighted candle at the other. The intensity of sound is modified by the condition of the atmosphere, sound being better propagated in calm than in windy weather; in the latter case, however, sound is better heard when transmitted in the direction of the wind than in the opposite direction. Finally, the intensity of sound is very much increased by the proximity of a sonorous body. Hence, the association of sounding-boxes with strings, as in the case

of the violin, guitar, etc., the increase in the loudness of the sound being then due to the fact that the box and air within it vibrate in unison with the strings as we shall endeavor presently to explain. The distance at which sounds are heard, depending upon their intensity, may be very great; thus, it is said that the report of the volcano at St. Vincent was heard at Demerara, 300 miles off, and the firing at Waterloo at Dover.[1]

Pitch of Sound.

Sounds are distinguished, as already mentioned, not only by their intensity or loudness, but by their pitch or height. The pitch of a sound can be shown to depend upon the number of vibrations made by a sounding body in a given time—a second, for example—sounds of low pitch being due to the aërial vibrations impinging upon the tympanic membrane following each other slowly, those of high pitch to the aërial vibrations following each other rapidly. Thus, for example, the pitch of the sound of a string four feet in length, sufficiently tensed, and of a given density and thickness vibrating 128 times in a second (Do^2,Ut^2, C^2 of piano), is low as compared with that of one two feet in length, vibrating 256 times in a second (Do^3,Ut^3,C^3), or an octavo above.[2] In the same way, the pitch of the sound of an organ-pipe four feet in length due to 128 vibrations per second (Do^2Ut^2) is low as compared with that of the sound of one two

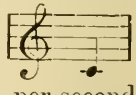
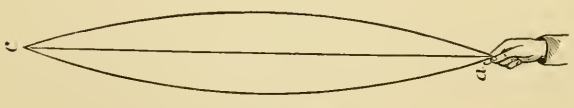
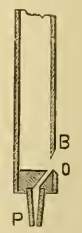


Fig. 477.



Vibration of string.

Fig. 478.



Organ-pipe.

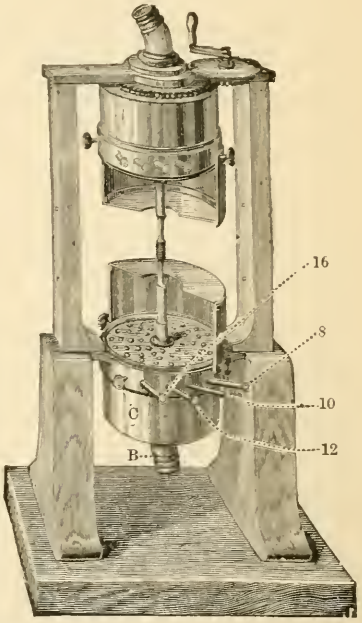
feet in length, due to 256 vibrations per second (Do^3Ut^3) or the octave above. It may be mentioned in this connection that, while in the case of the string it is the vibrations of the latter (Fig. 477) that give rise to the aërial vibrations affecting the auditory apparatus, in the case of the organ-pipe it is to the vibrations of the enclosed column of air that the aërial vibrations are due, as the current of air forced by the bellows through the mouth P B of Fig. 478 of the pipe in striking against the upper bevelled lip B, produces a shock, the air issues from the embouchure or space between the lips in an intermittent manner, the pulsations so produced in being transmitted to the air enclosed within the pipe in turn set it into vibration, which causes the sound. It will be observed, also, as might

[1] Ganot, Physics, Trans. by Atkinson, p. 175. London, 1870.

[2] If the 5th A of the piano be turned to vibrate 440 vibrations per second, instead of 426 times as assumed in text, then the middle C or Ut^3 will vibrate 264 times, and the lowest C 33 times per second.

have been anticipated on mechanical principles, that the number of vibrations, both in the case of the string and pipe, are inversely as the length, the number of vibrations in both cases being doubled by having the lengths, since, in the latter case, the amount of work to be done being one-half, it can be done in half the time, or double the work can be done in the same time. The distinction between intensity or loudness and pitch or height must be carefully borne in mind, being, as just shown, due to entirely different causes; a sound, therefore, may be a loud one, and yet be low in pitch; and, on the other hand, a sound may not be a loud one, and yet be high in pitch. In sounding the long string and long organ-pipe, apart from the intensity of the sound, and from the pitch of the note Do^2Ut^2, 128 vibrations per second, the same, therefore, in both cases, another and very marked difference is appreciable, and that by not especially musical ears, viz., the character or quality of the sound. Before considering, however, the quality of sound, or that in which the sound of a violin, for example, differs from that of a piano, and the sound of the latter from the sound of the organ-pipe, or, in general, that which distinguished the sounds of different kinds of musical instruments, let us first endeavor to explain how, by means of the siren, we are able to determine the number of vibrations to which the pitch of a sound is due. The siren—so called on account of its emitting sounds when under water in its original form as invented by Cagniard de la Tour—is a much more simple instrument than that we shall make use of, or the double siren of Helmholtz (Fig. 479). The principle upon which both instruments are constructed is, however, the same, since the siren of Helmholtz consists of two Dove sirens, the Dove siren in turn differing from that of Cagniard de la Tour (Fig. 481) in being provided with four series of orifices instead of one. Such being the case, let us begin our description of a double siren with that of a single Dove siren. Suppose, for example, that the lower Dove siren (Fig. 479) be taken apart, it will be seen that the tube B leads into the brass cylinder C, the top of which is closed by a brass plate, perforated with four series of holes disposed concentrically, the outermost

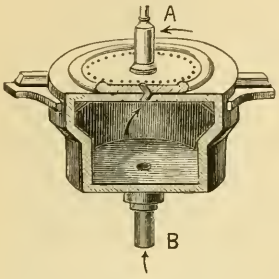
Fig. 479.



Helmholtz's double siren.

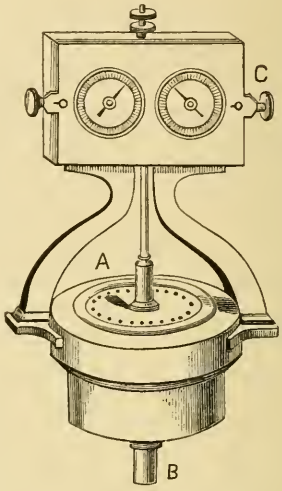
series containing 16, the next 12, the next 10, the next 8 orifices, the latter being opened or closed, respectively, by pressing in or pulling out the keys numbered correspondingly. It will also be seen that the brass disk, receiving in its center the steel axis x, is

Fig. 480.



Showing oblique opening in siren of Cagniard de la Tour.

Fig. 481.



Siren of Cagniard de la Tour.

also perforated with 16, 12, 10, and 8 orifices, disposed concentrically at the same distance from the center, and with the same intervals between them as those on the top of the cylinder C, the only difference between the two sets being that those passing through the top of the cylinder C, while oblique in direction (Fig. 480), are oppositely inclined to those passing also obliquely through the brass disk.

The two sets of orifices being so disposed to each other if air be forced by a pair of bellows through the tube B into the cylinder C, the air will issue from the latter not vertically but in side currents, which in impinging against the sides of the orifices of the disk will drive the disk around the axis x, held upright by means of a steel cap brought down on its upper end. As the disk turns around, its orifices, coming alternately over the orifice of the cylinder C and over the intervening spaces, the continuous current of air passing through the cylinder C is carved into discontinuous puffs, which at first follow each other so slowly that they may be counted. As the motion of the disk, however, increases the puffs of air succeed each other so rapidly that the air links them together as continuous musical notes, whose pitch can then be at once shown to depend upon the number of puffs of air or vibrations, by simply increasing or diminishing the rapidity of the rotation of the disk, the pitch of the note rising or falling accordingly. In order, however, to determine the number of puffs issuing from the orifices in a given time, a second, for example, they must be recorded. This is accomplished by providing the axis x at its upper part with a screw s (Fig. 482) which works into a pair of toothed wheels, the latter rotating as the disk and its axis turn, the number of rotations being indicated by

the hands on the dial plates (omitted in Fig. 479, but represented in Fig. 481), the hand of one dial plate making an entire revolution while that of the other passes over but one division of the graduated circumference. The process of recording can be started or stopped by simply pushing a button, which throws the wheel-work just mentioned into or out of action. In order, now, to show how by means of the siren we determine that the note Do^3, emitted by the string or organ-pipe two feet long, is due to the vibrations following each other at the rate of 256 vibrations a second, we force the air from the bellows through the cylinder C, the outermost series of 16 orifices being open until the disk rotates so rapidly that the sound produced by the siren is in unison with that emitted by the string or organ-pipe sounded at the same time. The sound of the siren and the string or pipe being then in perfect unison, we push the button and so set going the recording mechanism and let the siren sing for just one minute, then instantly stopping the recording, we observe by the hands of the dial plate the number of rotations the disk *d e* has made in that time. It will be found that the number is just 960; dividing this by 60 the quotient, or 16, will be the number of times that the disk has rotated in one second, but since 16 orifices were open in one rotation of the disk 16 puffs of air issued in succession from the siren, and consequently during 16 rotations 256 puffs of air. As the note Do^3, produced by the siren was due to the number of puffs or vibrations of air, and as the note of the siren was in unison with that due to the sounding of the string or pipe, the latter, or Do^3, must be also due to the same number of vibrations, viz., 256 vibrations per second. It will be remembered that while the outermost series of orifices, those which in the preceding experiment were supposed to be open, are 16 in number, the innermost series of orifices are only 8 in number. If the latter now be opened as well as the former by pushing in the key numbered 8, then two sounds will be simultaneously emitted by the siren, one of which, Do^3, is due, as before, to the rate of vibration being 256 per second, the other Do^2 an octave below, the rate being just half, or 128 vibrations per second, the air issuing from 8 orifices during one rotation of the disk, instead of from 16, as in the former case. The innermost and outermost series of orifices being open, then the rate of vibration of the two sounds is as 1 to 2. From what has just been said, it is evident, without further explanation, that if the innermost series of 8 orifices and the next series to it of 10 orifices be open, then the rate of vibration will be as 4 to 5—that is to say, of the two notes produced by the siren simultaneously, if one be Do^2, due to 128 vibrations per second, the other note will be Mi^2 E^2, due to 160 vibrations per second, and if the innermost series of 8 orifices and the third series from within outward, that of 12 orifices, be both open, then the rate of vibration of the two sounds will be as 2 to 3—that is, if Do^2 be one of the two notes heard simultaneously the other note will be Sol^2 G^2, due to 192 vi-

brations per second. It follows, therefore, that if the three innermost series of orifices, 8, 10, and 12, be open we will obtain the major chord C^2 E^2 G^2, Do^2 Mi^2 Sol^2, and if in addition at the same time the outermost series of 16 orifices be open C^2 E^2 G^2 C^3, which, as produced by the siren, is quite musical. The construction and manner of using a single Dove siren being now understood, there will be no difficulty in comprehending that of Helmholtz, it consisting, as already mentioned, of two Dove sirens. It must be mentioned, however, that the outermost series of orifices in the lower of the two sirens are 18 in number instead of 16, as in the single Dove siren we have just described, and that the orifices in the four series of the upper siren are respectively 9, 12, 15, and 16 in number. If, therefore, we wish to obtain by the double siren the major chord C^2 E^2 G^2 and C^3 at the same time, the series of orifices 8, 10 and 12 must be opened in the lower siren, and the series of 16 orifices of the upper siren, the air being allowed, of course, to pass from the bellows through both sirens, the number of rotations of the disks being recorded in the same manner as already described by wheelwork attached to the axis common to the two sirens, and omitted for simplicity in Fig. 479. It will be observed that the double siren is provided with resonance boxes the half of each of which has been removed in the figure, which greatly intensifies the fundamental sound. The upper siren is also connected with a toothed wheel and pinion turned by a handle, by which we are enabled to rotate the cylinder of the upper siren as well as the disk, the handle, etc., being so disposed that if it be turned to the right the orifices in the cylinder and in the disk will then pass over each other more quickly than if the cylinder was at rest, and if in the reverse direction more slowly, the pitch rising in the one case, the puffs succeeding each other then more rapidly, and falling in the other, following more slowly. The use of the dial and index underneath the handle will be illustrated hereafter. It is needless to say that by doubling all parts of the siren, etc., as done by Helmholtz,[1] that many varied combinations can be introduced, and that the general usefulness of the instrument has thereby been greatly increased.

Quality of Sound.

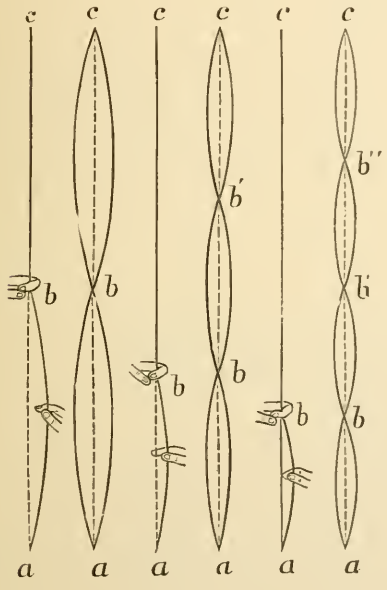
Every fundamental tone, whether produced by a string, column of air, reed, etc.—that is, a sound due to the string, for example, vibrating through the whole of its length (Fig. 477), may be accompanied by partial tones or overtones[2] due to the string vibrating through the half, third, fourth, etc., of its length (Fig. 482, (2), (4), (6)), and since the overtones, accompanying and reinforcing the fundamental tone, due to the sounding of the string of one instrument,

[1] On the Sensation of Tone, transl. by A. J. Ellis, p. 245. London, 1875.

[2] By the 1st, 2d, and 3d overtones, etc., will be meant in this chapter, tones due to vibrations whose rates are twice, three, or four times as rapid as that of the fundamental tone.

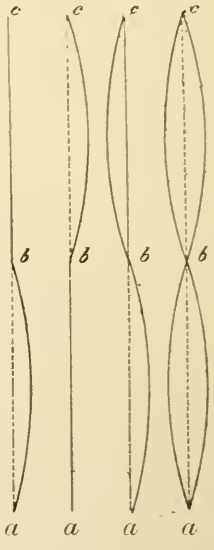
are not the same as those of another, or if in part the same, are then more or less accentuated, there arises in consequence a difference in the character of the sound as produced by the two instruments, very appreciable, even by unmusical ears, which is called their quality. Thus, for example, the sound of the string of a violin may be as loud as that of the piano, or of that of the vibrating column of air of the organ-pipe, or of that of the vibrating reed of the oboe, the pitch of the particular note emitted by the four instruments may be the same, the number of vibrations per second to which the note

FIG. 482. FIG. 483.



(1) (2) (3) (4) (5) (6)

Formation of nodes and ventral segments. (TYNDALL.)



(1) (2) (3) (4)

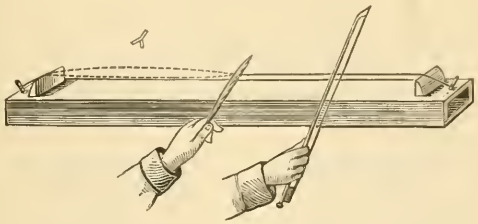
Vibrations of tube. (TYNDALL.)

is due being equal in all four instances, and yet no one fails to appreciate the difference in the character or the quality of the sound, the overtones reinforcing the fundamental note being different in each instance. Inasmuch, however, as the thorough understanding of the conditions, upon which the quality of sound depends is not only important, but absolutely essential, in comprehending the manner in which the vowels are produced by the larynx, for example, let us endeavor to explain a little more in detail how these partial vibrations, to which the overtones are due, come to be superimposed upon the fundamental one, and how their presence can be detected. Let *c a* (Fig. 483) represent a long India-rubber tube fixed at the one end, and free at the other. By taking hold of the free

end, stretching the tube a little, and properly timing the impulses, the tube can be made to swing to and fro, to vibrate as a whole, as represented in Fig. 477. Stop the motion, and now, by a jerk, raise a hump upon the tube, the hump will be observed to run along the tube *a b*, *b c* (Fig. 483, (1), (2)), and having reached the fixed end of the tube *c*, will then run back again, but in the reverse direction. But just as the latter *c b* (3) starts at *c*, let the tube be jerked again, so as to start the hump *a b* (3) at *a*, then by the time that the foremost part of the hump beginning at *c* arrives at *b*, that beginning at *a* will also have reached *b*, the effect of which will be that the point *b* will remain at rest. For the hump *a b* (3) in moving on to *c* must tend to move the point *b* to the right, and the hump *c b* moving on to *a* must tend to move the point *b* to the left, the consequence of which is, that the point *b*, in being acted upon by equal and opposite forces, will not move at all. Such being the case, the two halves, *ab*, *bc* of the tube *b c*, will vibrate as if they were independent of each other (Fig. 483 (4)). The point *b* at rest is known as the node, the vibrating parts *a b*, *b c* as the ventral segments, twice the length of a ventral segment constituting a wave, the latter being made up by both the hump and the depression following the same. By experimenting a little, it will be soon found that the tube *a c* (Fig. 482) can be so swung as to form two nodes with three ventral segments (4), or three nodes with four ventral segments (Fig. 482, (6)), and so on, the tube vibrating in thirds, fourths, etc., of its length, and a little reflection will make it clear that the cause of the formation of the nodes, or points of rest, and of the string in consequence vibrating in its aliquot parts, is precisely the same as that just given in the case of the formation of one node and two ventral segments. Let us now modify the preceding experiment slightly by encircling the tube *a c* at its center (Fig. 482, (1)) with the thumb and forefinger of one hand, and, taking hold of the middle of the lower half of the tube *a b* with the other hand, pull it aside. It will be observed that one node is formed, and two ventral or vibrating segments (2), the upper half of the tube vibrating as well as the lower. Experimenting in this way, but encircling, however, the tube at one-third (3) or one-fourth (5) of its length, and pulling the lower third (3) or lower fourth (5) of the tube away by seizing them, respectively, at their centers, the tubes will be oscillated, so that two nodes with three ventral segments (4) or three nodes with four ventral segments (6), will be formed, as the case may be, the vibrations of the string through the space encircled by the thumb and finger, a distance of one inch, acting upon the upper part of the tube exactly as the hand acted when it caused the tube to swing as a whole. In precisely the same manner, by placing a feather (Fig. 484) upon the center of the stretched violin-string, just as we encircled the tube with the thumb and finger, and drawing a bow across the center of the half of the string instead of pulling it aside with one hand, the

string will be made to vibrate in halves, as shown by the little paper rider being thrown off. Similarly, by touching the string with a feather at a third (Fig. 485), or a fourth (Fig. 486) of its

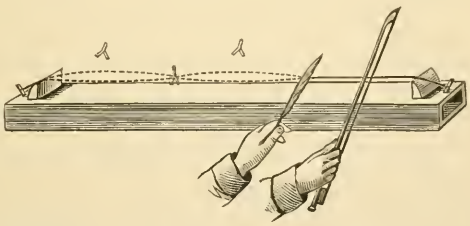
FIG. 484.



Formation of one node and two ventral segments. (TYNDALL.)

length, and drawing the bow across the center of the right hand third or fourth of the string the string will vibrate in thirds or fourths, two nodes with three ventral segments, or three nodes with four

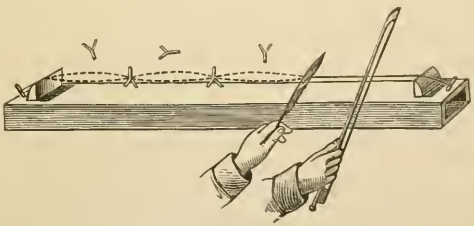
FIG. 485.



Formation of two nodes and three ventral segments. (TYNDALL.)

ventral segments being formed, as shown by the two or three red paper riders placed upon the vibrating parts being tossed off, and the one or two blue ones remaining on the string being situated

FIG. 486.

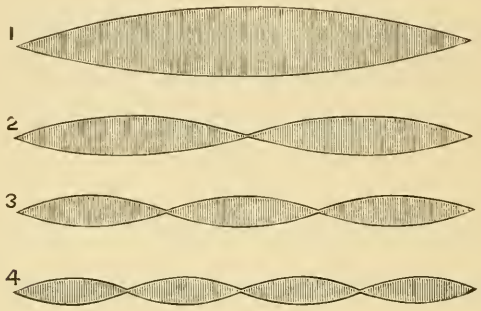


Formation of three nodes and two ventral segments. (TYNDALL.)

at the nodes, or points of rest. A beautiful way of demonstrating the presence of nodes and ventral segments made use of by the author in addressing a large audience, is to place a string

connected at one end with the prong of a tuning fork, and at the other with a peg, by which it can be loosened or tightened in front of the calcium light lantern, an appearance such as that represented in Fig. 487 being presented when the fork is sounded, according

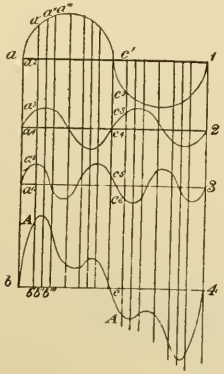
Fig. 487.



Nodes and segments of a vibratory string as shown by lantern.

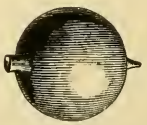
to the extent to which the string is tensed. While the string may vibrate as a whole, or in halves, thirds, fourths, fifths, etc., separately, as we have just shown, as a matter of fact, the string usually in vibrating breaks up, so to speak, into its aliquot parts, the superimposing of which vibrations upon the fundamental vibration of the string—that is, of the vibration due to the swinging of the

Fig. 488.



Compound waves. (McGregor Robinson.)

Fig. 489.



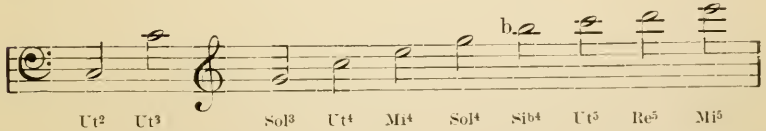
Resonator of Helmholtz.

string, as a whole, gives rise to a resultant vibration, which has been shown to be equal to the algebraic sum of all the vibrations,[1] as represented in Fig. 488 in which the lower curve represents the compound vibration resulting from the blending of the three upper curves, representing, respectively, simple vibrations, whose ratio is as 1, 2, 3. Of course, it must not be supposed that sounds, simple or compound, are due to curves like those depicted in Fig. 488; the latter are simply graphic representations of

[1] Helmholtz, op. cit., p. 43.

waves of sound, which, as we have seen, consist of condensations and rarefactions of the air. That the tone due to the sounding of a string of the piano, such as Do^2, vibrating 128 times per second, is not a simple, but a compound tone, will be appreciated by a trained musician, whose sensitive ear enables him to distinguish some at least of the overtones accompanying the fundamental tone. Any one, however, can convince himself that such a tone as that of Do^2 sounded by the piano, as elicited by singing the corresponding note, is a compound one, resulting from the blending of the fundamental tone with overtones, the latter being due to the partial vibrations of the string, as the former is to the oscillating of the string as a whole, by adapting to his ear in succession each one of the series of nine resonators, of which one is represented in Fig. 489, devised by Helmholtz,[1] and so constructed as to intensify the sound of each particular overtone accompanying the fundamental tone, that overtone being then heard alone. Thus, for example, the largest resonator, marked Ut^3, being applied to the ear, let the note Ut^2 due to 128 vibrations a second be sounded; the first overtone or harmonic, or the octave above Ut^3, 256 vibrations per second, will be heard, due to the string vibrating in halves, the sound distinctly heard with the resonator being the same as if the note Ut^3 had been sounded.

Applying the next largest resonator, marked Sol^3, to the ear and sounding the Ut^2 string on the piano the second overtone, the twelfth above the fundamental, or Sol^3, will be heard, due to the string vibrating in thirds, the sound heard being the same as if the note Sol^3 had been sounded. Adapting in succession the remaining resonators gradually diminishing in size, and marked respectively Ut^4 Mi^4, Sol^4 Si^{b4} Ut^5, Re^5 Mi^5, the 3d, 4th, 5th, 6th, 7th, 8th, and 9th overtones due to the string or harmonics will be heard vibrating in fourths, fifths, sixths, etc., the sounds heard with the resonators being the same as if the notes Ut^4 Mi^4 Sol^4 Si^{b4} Ut^5 Re^5 Mi^5 had been separately sounded, or as expressed in musical notation as follows, Do^2 Ut^2 being the fundamental tone:



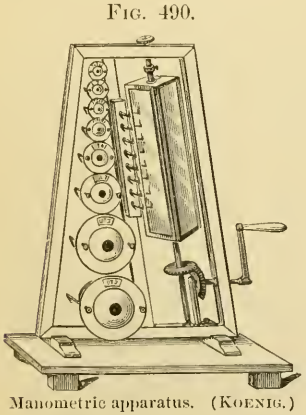
It is obvious, therefore, why when the notes Ut^3 Sol^3 Ut^4 are sounded on a musical instrument at the same time with Ut^2, the resulting sound should be harmonious, since these three sounds reinforce respectively the first, second, and third overtones due to the string vibrating in halves, thirds, and fourths respectively. In the same way, Mi^4 Sol^4 Si^{b4} Ut^5 Re^5 Mi^5 reinforcing the overtones due

[1] Op. cit., p. 68.

to the string Ut^2 vibrating in fifths, sixths, sevenths, eighths, and ninths, when sounded with Ut^2, will also give a harmonious sound.

Having described the manner in which partial vibrations are formed, and how in being superimposed upon the fundamental vibration a resultant vibration arises, and how the overtones due to the partial vibrations in being blended with the fundamental tone due to the fundamental vibration give rise to a compound tone, it becomes evident without further explanation, that by means of the Helmholtz resonators we can analyze any sound, and demonstrate whether it be a simple or compound one, and, if the latter, what overtones are present, and in this way show on what the quality, timbre, or klangfarbe of the sound depends. Thus, for example, the quality of the sound of the piano, as compared with that of the violin, depends upon the fact that in the case of the latter, when bowed, though the first six overtones or harmonics are present, as in the case of the piano, they are so faintly sounded as to be overpowered by the seventh, eighth, ninth, and tenth overtones. The overtones in the case of an open pipe are not the same as in the case of a closed one; those of the clarionet differ from those of the oboe, and so through the whole range of orchestral instruments. Inasmuch, however, as in addressing a large audience, from the nature of the case, it is impossible for each one individually to make use of the resonators and satisfy himself of the existence of overtones upon which the quality of a sound depends; the author is accustomed to demonstrate the same by means of Koenig's manometric apparatus.[1] The latter (Fig. 490) consists of a frame supporting a number of resonators each of which leads by a narrow India-rubber tube into a small chamber, completely divided into two, by an India-rubber partition. The posterior part of the chamber is in communication with the resonator, the anterior part provided with a gas jet with a reservoir containing gas, led thither by an ordinary gas pipe. Each resonator is connected in this way with its own gas chamber and burner, the burners being all placed in a row, one above the other. Opposite the gas burners is a long mirror with four reflecting sides, at right angles to one another, which can be revolved on an almost perpendicular axis by a toothed wheel arrangement. Turning on the gas, and lighting it as it issues from the jets in the chambers connected with the resonators, and revolving the mirror, the light reflected from the surfaces of the latter appears as continuous bands. If, however, the air in any one of the

Fig. 490.

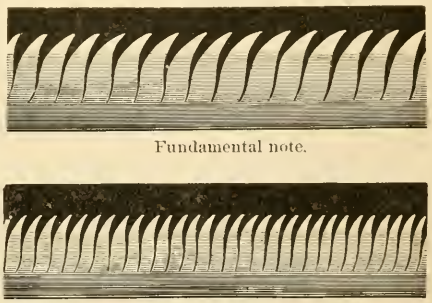


Manometric apparatus. (Koenig.)

[1] Rudolph Koenig, Quelques Experiences d'Acoustique, p. 73. Paris, 1882.

resonators be thrown into vibration, then the India-rubber partition of the chamber separating, on the one hand, the air continuous with that of the resonator, and, on the other, the gas, will vibrate, and the gas and flame thrown into agitation, the particular band of light, the corresponding band of light, becoming segmented. Let now a tuning fork Ut^3, vibrating 256 times a second, be sounded in front of the apparatus; at once the flame in connection with the resonator marked Ut^3, will become segmented, but the remaining flames will still appear as continuous bands of light, since if the tuning fork be properly bowed the sound produced will be a pure, simple tone, unaccompanied with overtones. Let now, however, the Ut^3 Do^3 of the piano, or an open organ-pipe two feet long, giving, therefore, the same fundamental note, be sounded, and immediately some of the remaining bands of light will become segmented, as well as the one connected with the resonator marked U^3, since the air of the resonators with which they are in connection has been thrown into vibration by the particular overtones present, as, for example, in Fig. 491, a, b, representing respectively the flames due to the fundamental and octave above it. In this way an optical demonstration can be given of the fact that the quality of the note of any musical instrument depends upon what particular overtones or harmonics accompany the fundamental, and, as we shall see presently, of the manner in which the vowel sounds are produced by the human voice. As it is important that the manner in which resonators reinforce or intensify sounds should be understood, a brief account of the cause of resonance in general may be as appropriately considered here as elsewhere.

Fig. 491.



a

Fundamental note.

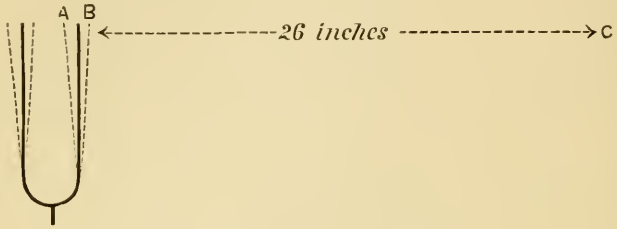
b

Octave of preceding.

It is well known that the velocity with which sound travels in air at the freezing temperature is 1,090 feet in a second, the velocity increasing about two feet for every additional degree of heat Centigrade (1.8° F.). Let us suppose that the temperature of the surrounding atmosphere be 8.5° Cent. (47.3° F.), and that a tuning fork vibrating 256 times per second be sounded; it is obvious that if, at the end of the second, the sound has reached a distance of 1,101 feet, then each vibration must have been 52 inches long, since 52 multiplied by 256 gives 1,101 feet, and as a vibration or wave of sound consists, as we have seen, of a condensation and rarefaction, the condensation and rarefaction must have been both just 26 inches in length. That is to say, as the prong of the tuning fork (Fig. 492) moves from A to B, a distance of perhaps the

one-twentieth of an inch, it generates the one-half of a sonorous wave, the condensation, the foremost point of which reaches a distance of twenty-six inches, at the same instant that the prong of the fork reaches B, and as the prong of the fork moves

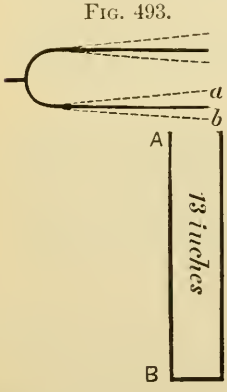
FIG. 492.



Tuning fork vibrating. (TYNDALL.)

back from B to A, the other half of a sonorous wave, is generated, the rarefaction or the part progressing backward toward B, the second condensation progressing forward at the same time toward C. Such being the case, let the tuning fork now be sounded over a jar (Fig. 493), of which the column of air within, from top to bottom, measures just thirteen inches, or one-fourth the length of the vibration or wave due to the sounding of the fork. It follows from what has just been said, that during the time the prong of the fork moves from *a* to *b*, the condensation, the air which it produces runs from the top of the jar to the bottom, thirteen inches, and from the bottom to the top, thirteen inches, or twenty-six inches in all, the reflected wave reaching the prong of the fork just as the latter reaches *b*; and similarly, that during the time the prong returns to *a* from *b*, the rarefaction to which it gives rise runs down from the top of the jar to the bottom, and up again, also a distance, in all, of twenty-six inches.

FIG. 493.



Tuning fork vibrating in unison with jar.

The vibrations of the fork being, therefore, perfectly synchronous with the vibrations of the aërial column within the jar, the motion will accumulate in the latter, and spreading out into the room, the sound will be greatly augmented as everyone will appreciate, when the tuning fork is sounded first at some distance from, and then over the mouth of the resonating jar. From what has just been said, it necessarily follows that if we sound other tuning forks, vibrating at different rates, the length of the column of air must be varied accordingly if we wish to make use of the latter as a resonator. It is for this reason that the resonators made use of in

demonstrating the presence of overtones are of different size, and that the resonators of Koenig's manometric apparatus are so constructed, that by drawing them out to varying distances, the sound that each resonator will reinforce will then be different. It is on account of its resonating qualities that, in sounding a bell, the latter is often placed near the mouth of a jar, by means of which the intensity of the sound is very much increased. The ancients were well acquainted with the efficacy of such aids in intensifying sound, resonant brass vessels being placed, according to Vitruvius, in their theatres to strengthen the voices of the actors. It is on account of the resonating properties of sounding boards, that the latter are associated with musical instruments, and that the stethoscope also has proved in the hands of the clinician such an aid in the diagnosis of disease by auscultation.

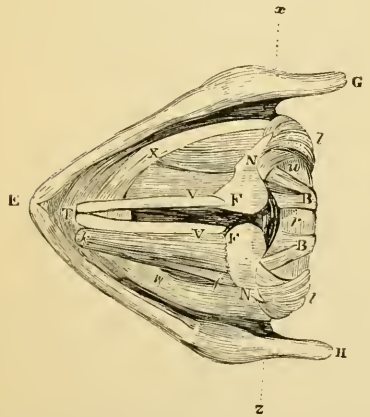
Having shown that sounds are produced by the vibrations of plates, bells, strings, pipes, reeds, membranes, etc., and how the same are distinguished by their intensity, pitch, and quality, let us turn now to the consideration of the larynx, and by means of the principles just established, endeavor to determine what kind of an acoustical instrument the larynx is and how the voice is produced by it.

CHAPTER XLII.

THE LARYNX, AND THE PRODUCTION OF THE VOICE AND SPEECH.

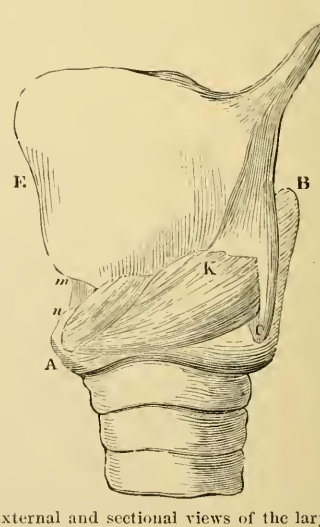
The larynx, the organ of the voice, situated at the top of the trachea and below the root of the tongue and the hyoid bone, consists of a framework of cartilages, connected by ligaments, provided with muscles, blood vessels, and nerves, and lined with mucous membrane. The cartilages of the larynx are nine in number, three single and symmetrical pieces, the thyroid, cricoid, and epiglottic, and three pairs, the arytenoid, corniculа laryngis, and cuneiform; the last two pairs are, however, very small. The thyroid (Fig. 494),

Fig. 494.



Bird's-eye view of larynx from above. G E H, the thyroid cartilage, embracing the rings of the cricoid, *r u X w*, and turning upon the axis, *x z*, which passes through the lower horns. N F, N F, the arytenoid cartilages connected by the arytenoideus transversus. T V, T V, the vocal membranes. N X, the right crico-arytenoideus lateralis (the left being removed). V *k f*, the left thyro-arytenoideus (the right being removed). N*l*, N*l*, the crico-arytenoidei postici. B, B, the crico-arytenoid ligaments.

Fig. 495.

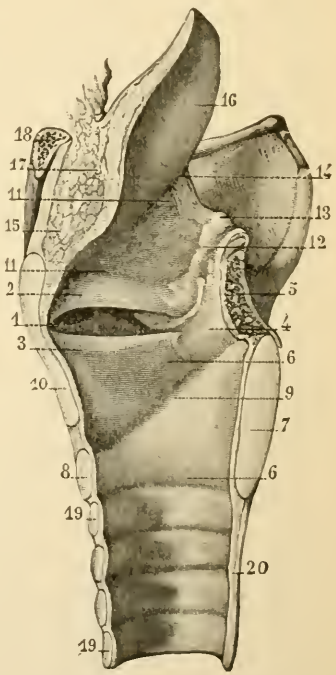


External and sectional views of the larynx. A *n* B. The cricoid cartilage. E C G. The thyroid cartilage. G. Its upper horn. C. Its lower horn, where it is articulated with the cricoid. F. The arytenoid cartilage. K. Crico-thyroid muscle.

the largest of the cartilages of the larynx (Figs. 494, 495), consists of two lateral ring-like plates or alæ, continuous in front, but diverging behind. The angular projection in front, surrounded by a deep notch much more marked in the male than in the female, and in some men more than others, is known as Adam's apple, while the blunt processes, into which the posterior angles are prolonged, are called the superior and inferior horns, of which the superior are the larger, and are connected by ligaments with the hyoid bone. The

cricoid cartilage, resembling in shape a seal ring, is situated between the thyroid and the first ring of the trachea, with the latter of which it is connected. While quite narrow in front, the cricoid cartilage deepens considerably posteriorly, and at the back part of its upper border, articulates by means of two convex oval prominences with the arytenoid cartilages, and laterally through two circular facets with the inferior horns of the thyroid cartilage. The arytenoid cartilages are two three-sided recurved pyramids, resting by their bases upon the posterior and highest portion of the cricoid cartilage. The apex of each arytenoid cartilage is usually surmounted by a yellowish cartilaginous nodule, the corniculа laryngis or cartilages of Santorini, while the folds of mucous membrane, extending from the summit of the arytenoid cartilages to the epiglottis, contain also two small yellowish cartilaginous bodies, the cuneiform cartilages, or cartilages of Wrisberg. The posterior lateral corner of each arytenoid cartilage presents a blunt projection for the attachment of muscles, the processus muscularis and the anterior lower and median part a surface for the posterior attachment of the vocal membrane, the "processus vocalis." The remaining cartilages of the larynx, the epiglottis, consisting really of fibro-cartilage, somewhat spoon-shaped in form, while free at its broad extremity, is attached at its narrow end by a band of fibro-elastic tissue to the thyroid cartilage within the entering angle of its two halves, and to the tongue, hyoid bone, and arytenoid cartilages by the glosso-epiglottidean, hyo-epiglottidean, and aryteno-epiglottidean folds, respectively.

FIG. 496.



Longitudinal section of the human larynx, showing the vocal membranes. 1. Ventricle of the larynx. 2. Superior vocal membrane. 3. Inferior vocal membrane. 4. Arytenoid cartilage. 5. Section of the arytenoid muscle. 6, 6. Inferior portion of the cavity of the larynx. 7. Section of the posterior portion of the cricoid cartilage. 8. Section of the anterior portion of the cricoid cartilage. 9. Superior border of the cricoid cartilage. 10. Section of the thyroid cartilage. 11, 11. Superior portion of the cavity of the larynx. 12, 13. Arytenoid gland. 14, 16. Epiglottis. 15, 17. Adipose tissue. 18. Section of the hyoid bone. 19, 19, 20. Trachea.

The cavity of the larynx (Fig. 496) is divided by the glottis, or rima glottidis, that is, the space between the vocal membranes, "rima vocalis," and between the vocal processes, "rima respiratoria," into an upper and lower compartment. The upper compartment commencing with the pharynx by the superior aperture of the larynx, contains the ventricles and the upper or so-called false vocal cords. The lower compartment passes inferiorly

into the trachea without any observable constriction between them. The mucous membrane lining the cavity of the larynx, continuous with that of the pharynx and trachea, extending from the epiglottis to the tongue and arytenoid cartilages as the glosso-arytenoid epiglottidean folds, descends from the superior aperture and is reflected at each side outwardly and upwardly as a pair of pouches, the ventricles of the larynx, oval recesses communicating by a transverse elliptical orifice with the interior of the larynx, and prolonged upward and outward as the laryngeal pouches. The upper edge of the ventricle, somewhat prominent through the presence of connective tissue, is known as the false vocal cord, since it is not concerned in the production of the voice, the lower edge corresponding with the upper border of the vocal membrane or true vocal cord, as it is often improperly called, and upon the vibration of which the production of the voice depends. From the ventricles the mucous membrane passes downward, lining the vocal membrane, cricoid cartilage, and finally becomes continuous with that of the trachea. The mucous membrane of the larynx is soft, thin, and pale red, its epithelium being of the ciliated columnar form, except upon the so-called vocal cords, where it is stratified like that of the pharynx and mouth. That part of the mucous membrane situated at the base of the epiglottis being thickened, gives rise to a slight prominence, the so-called "cushion." While adhering tightly to the epiglottis, the vocal membrane, and the interior of the cricoid cartilage, the mucous membrane in other parts of the larynx is loosely attached to the subjacent parts by connective tissue.

The vocal membranes (Figs. 494, 496), 15 mm. (about seven lines) long in the male and 10 mm. (five lines) in the female, bounding the anterior third of the aperture of the glottis, and consisting of elastic tissue, may be regarded as extending from the front and sides of the upper border of the cricoid cartilages, upward to the bases of the arytenoid cartilages, and to the lower part of the entering angle of the thyroid. The lower portion of each vocal membrane is the strongest, and may be seen at the front of the larynx in the interval between the thyroid and cricoid cartilages. The lateral portions are thin and are separated by the thyroid and arytenoid muscles from the alæ or wings of the thyroid. The upper margins of the vocal membranes—that is, the parts corresponding in position to the lower edges of the ventricles, extending on either side from the anterior prominent angle of the base of the arytenoid cartilages to the entering angle of the thyroid, being somewhat thickened, are usually described as the "true vocal cords," as contrasted with the false vocal cords, or the upper edges of the ventricle. As a matter of fact, however, apart from the vocal membrane, of which they are the upper thickened edges, no such organs as vocal cords exist. That the whole vocal membrane consists of elastic tissue is readily shown by the yellowish color of the tissue being distinctly seen through the overlying mucous membrane, which

in this situation is quite thin. The essentially membranous character of the vibrating portion of the larynx is well seen in the case of the elephant, in which animal the vocal membranes are two elastic bands almost two inches in length and nearly three-quarters of an inch in breadth. Inasmuch as the vocal membranes extend from the arytenoid cartilages to the thyroid, it is evident that if these cartilages approach or recede from each other the vocal membranes will be relaxed and tensed accordingly, and that if the arytenoid cartilages be rotated backward or forward, the vocal membranes will recede or diverge from each other, or will approach and become parallel. Such changes in the tension of the vocal membranes and in the form of the glottis, just referred to, are, as a matter of fact, brought about through the action of the intrinsic assisted by the extrinsic muscles of the larynx upon the thyroid and arytenoid cartilages. Thus the crico-thyroid muscle (Fig. 495) arising from the front and side of the cricoid cartilage to be inserted in the lower border of the thyroid in drawing the latter downward and forward, and therefore away from the arytenoid, tenses the vocal membrane. On the other hand, the thyro-arytenoid muscle (Fig. 494, V *k f*) arising from the inner surface of the thyroid cartilage to be inserted into the outer surface and base of the arytenoid cartilage, in drawing the latter forward relaxes the vocal membrane.

The influence exerted by the crico-thyroid and thyro-arytenoid muscles upon the tension of the vocal membranes, as just described, can be conveniently illustrated by the model represented in Fig. 497, in which the vertical bar represents the cricoid cartilage, the cross piece *c b* the thyroid cartilage, and the string *b a* the vocal membrane, and the cords and weights B A the thyro-arytenoid and crico-arytenoid muscles respectively. It is obvious that when the bar *b c* is pulled down to the position *c d* by the weight A, the elastic band *a b* is put on the stretch, and when elevated by the weight B, the elastic band *a b* is relaxed.

Fig. 497.

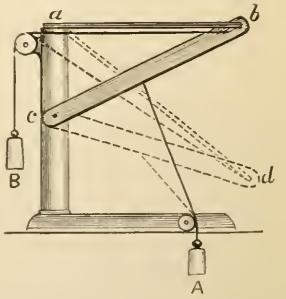
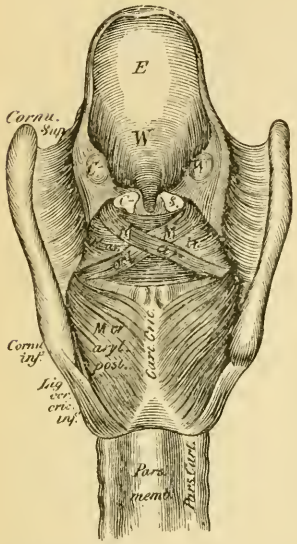


Diagram of a model illustrating the action of the muscles of the larynx. (Huxley.)

It is also probable that the vocal membranes are approximated and their form and thickness modified by the contraction of these muscles. The effect of the contraction of the crico-thyroid muscles in stretching the vocal membranes is increased by the simultaneous contracting of the arytenoid, crico-arytenoid, postici, and sterno-thyroid muscles, that of the thyro-arytenoid in relaxing the vocal membranes by the action of the crico-thyroid lateralis and thyro-hyoid muscles. The posterior crico-arytenoid

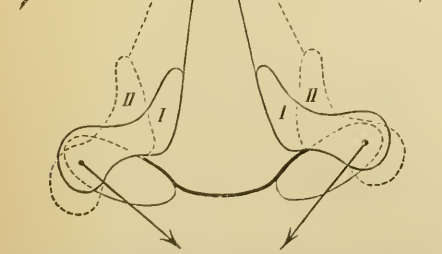
muscle (Fig. 498), so called on account of its arising from the posterior surface of the cricoid cartilages to be inserted into the external angle of the base of the arytenoid cartilage, in rotating the latter backward not only widens the glottis (Fig. 499), but, as just mentioned, also assists in tensing the vocal membrane. The lateral crico-arytenoid muscles (Fig. 500) lying under the wing of the thyroid cartilage, arising from the upper lateral border of the cricoid to be inserted into the external angle of the base of the arytenoid cartilage, in contracting rotate the latter forward and press together their inner edges, and not only narrow the glottis, but assist in relaxing the vocal membrane. The arytenoid muscle, consisting of transverse and oblique fasciculi, being attached to the posterior concave surface of the arytenoid cartilages, in contracting draw the latter together and so narrow the glottis. In addition to the muscles just described, there are usually found a few muscular fibers passing from the epiglottis to the thyroid and arytenoid cartilages, known as the thyro-

Fig. 498.



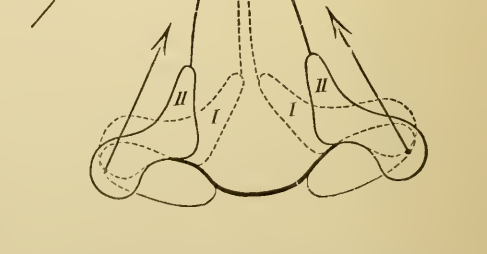
Larynx from behind with its muscles. *E.* Epiglottis, with the cushion W. *C* (*W*) Cartil. Wrisbergii. *C. S.* Cartil. santorinianæ. *C. c.* Cartil. cricoidea. Cornu sup. cornu inf. cartilaginis thyreoideæ. *M. ar. ir.*, Musculus arytenoideus transversus. *Mm. ar. obl.* Musculi arytenoidei obliqui. *M. cr. aryt. post.* Musculus crico-arytenoideus posticus. *Pars. cart.* Pars cartilaginea. *Pars memb.* Pars membranacea trachæ. (Landois.)

Fig. 499.



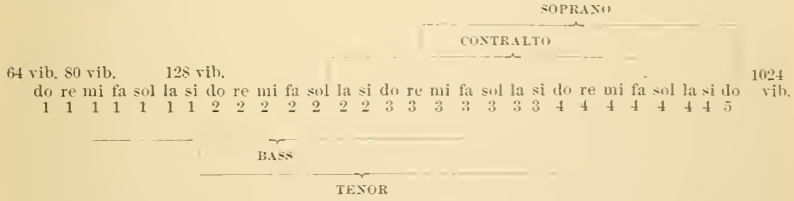
Lozenge shape of the glottis, produced by the action of the posterior crico-arytenoid muscle. (Kuss.)

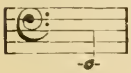
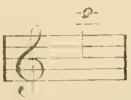
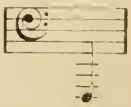
Fig. 500.



To illustrate action of crico-arytenoid lateralis muscle. (Kuss.)

and aryteno-epiglottidean muscles, whose functions appear to be to depress the epiglottis, and compress the laryngeal pouches respectively. Such being, in brief, the general structure of the larynx, it follows, from what was said in the preceding chapter, that if the air expired from the lungs and ascending in the trachea in passing through the glottis throws the elastic vocal membranes into vibration, a sound, the voice, will be produced, the character of which will depend upon the tension of the vocal membranes, shape of the glottis, etc., just as we can produce a sound by forcing air by means of a bellows through a glass tube, over the mouth of which have been stretched two elastic membranes. Lest, however, the analogy of the bellows and pipe to the lungs and trachea might suggest the idea of the larynx acting as an organ-pipe, or that the misnomer vocal cords might give the impression that the larynx acts as a stringed instrument, let us compare the range of the voice, on the one hand, with that of notes as produced by organ-pipes and strings on the other, and it will then become evident that the larynx does not act like either. The range of the human voice in the two sexes, and of the bass and tenor voice in the male and female, can be most conveniently illustrated by musical notation after Müller,[1] as follows:



from which it will be seen that the voice ranges ordinarily from mi_1  80 vibrations per second, the lowest note of the male bass voice, to do_5 Ut_5  1,024 vibrations per second, the highest note of the female soprano or tenor, though it should be mentioned that some bass voices reach the fa_1 42.6  vibrations per second of the octave below the above scale or even lower, and some soprano voices the sol_5 1,536 vibrations

[1] Physiology, trans. by Baly, Vol. ii., p. 1030. London, 1842.

per second above and even higher. The human larynx being capable, therefore, in the case of a man of emitting ordinarily a note due to 80 vibrations a second, and in a woman of one due to 1,024 vibrations, would have to be over five feet long and six inches long, respectively, if it acted like an organ-pipe, since that would be the length of the pipes giving those notes, the notes of an eight-foot pipe and six-inch pipe being due to 64 and 1,024 vibrations a second, respectively. Similarly no notes as deep as those of the bass voice can be produced by strings as short as the vocal membranes, however the latter may be relaxed.

Further, apart from the fact of the vocal membranes being too short to produce bass notes on the supposition that they act like strings, the E string of the double bass, for example, vibrating 41¼ times per second, the ratio of the vibrations of the vocal membranes to the weight extending them is not the same. Thus, for example, while it is well known that the vibrations of a string are doubled by quadrupling the extending weights, the number of vibrations being proportional to the square root of the weight, the vibrations of the vocal membranes, as shown experimentally by Müller,[1] are not so doubled by quadrupling the extending weight, the vibrations not reaching the octave above, as in the case of a string, by several semitones. On the other hand, it has been shown by Müller that the vibrations of the vocal membranes are governed by the same law as that regulating the vibrations of reeds or tongues, when the latter are associated with pipes. The latter qualification must be borne in mind, since in reed instruments like the accordion, concertina, seraphine, harmonium, etc., in which the reed or tongue vibrates in a sort of frame that permits of the air passing out on all sides of it through a narrow channel, thereby increasing the strength of the blast, the sound produced is due to the vibration of the reed or tongue alone, and is regulated entirely by the length and elasticity of the latter. In reed instruments like the clarionet, bassoon, and oboe, however, in which the single or double reeds are associated with pipes, the air setting the reed in vibration traverses the whole length of the pipe before escaping into the atmosphere, and consequently the sound produced is due to the vibrations of both reed and pipe combined, and not to either of them singly—the two sounds accommodating themselves to each other in such a way that only one sound is heard, the fundamental being neither always that of the reed alone nor of the pipe alone. In the case of the clarionet, in which the reed is a single broad tongue, and in the oboe and bassoon, in which the reeds are double and somewhat spoon- or spatula-shaped, the different notes are produced by closing or opening a series of holes, the position of which has been determined by experiment. In the reed pipes of the organ, however, in which the reed is inserted into the pipe through a plug, each note has a separate pipe. It was established more especially by

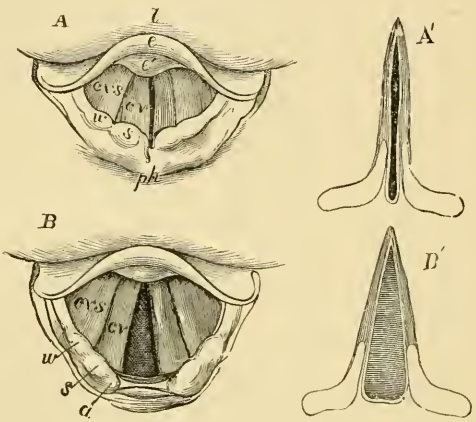
[1] Op. cit., p. 985.

Weber[1] that reeds associated with pipes, as in the case of the voice and of the instruments just mentioned, possess certain well-marked properties by which they can be at once distinguished from other musical instruments, such as organ-pipes, flutes, etc., and with which, in the case of the voice, they may be confounded. Among the most important of such properties may be mentioned, 1st, that the pitch of a reed, though it cannot be raised, may be lowered by joining it to a tube, but at the utmost by not more than an octave; 2d, that the fundamental note of the reed so lowered may be raised again to its original pitch by a lengthening of the tube, the latter then yielding the same fundamental note as the reed of the instrument without the tube, whilst by a further lengthening the pitch is again lowered, and by a still further lengthening raised again; 3d, that the length of the tube necessary to lower the note to any given pitch, depends on the relation existing between the rapidity of the vibrations of the tongue of the reed and those of the column of air in the tube, each taken separately. Accepting the above as the essential conditions which an instrument must fulfill in order to constitute a reed instrument, Müller[2] showed that the larynx, in fulfilling the same, must be regarded as a reed instrument, the vocal membranes being comparable to membranous vibrating tongues. The conclusion just arrived at, based upon acoustic principles, that the larynx is a reed instrument, is fully borne out, not only by the fact that in several instances persons rendered voiceless by the loss of their larynx, have been enabled to speak, so as to be perfectly heard through the introduction into the trachea of a tube containing a reed, but also by observing directly the larynx during phonation with the laryngoscope. Among the first to investigate the larynx in this way was Manuel Garcia,[3] so distinguished as a singing teacher, whose experiments were made principally with the view of determining the scientific principles upon which the teaching of singing should be based, and which, up to that time, had been taught by purely empirical methods. The difficulty of observing the vocal membranes during phonation on account of the epiglottis hiding so much of their anterior portions, especially in the production of high notes, is a familiar fact to those in the habit of using the laryngoscope. The perfect control, however, possessed by Garcia over his own vocal organs, together with the skill with which he examined them in his own person, enabled him finally to determine very satisfactorily the changes actually undergone by the glottis and vocal membranes during singing, the accuracy of the observations, models of scientific research, being fully confirmed by later observers. The changes in the glottis during ordinary breathing (Fig. 501, A A′) having been already described, it will be only necessary in this connection to recall the fact, that during inspiration the glottis, through the action of the crico-arytenoidei

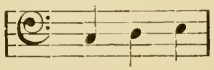
[1] Poggendorf, Annalen, xvi., xvii. [2] Op. cit., pp. 985, 999, 1023.
[3] Proc. of Royal Society Lond., 1856, Vol. vii., p. 399.

postici muscles, is widely dilated, and that during expiration, the larynx appearing to be passive, the air is gently forced out through the glottis by the expiratory movements of the chest. Garcia having first noticed the movements of the larynx during his ordinary breathing, observed next that just at the moment of making a vocal effort, his glottis underwent an entire change, the arytenoid cartilages being so approximated that the vocal cords were brought parallel to each other (the distance separating them, it may be here

FIG. 501.

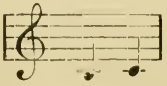


A. The glottis during the emission of a high note in singing. *B*. An easy or quiet inhalation of air.

mentioned, not exceeding the one-twelfth of an inch), the glottis then appearing as a narrow slit (Fig. 501, B B′). The glottis being thus prepared, so to speak, for the emission of a note through the action of the expiratory muscles, air is forced through the slit or chink, the effect of which is that the vocal membranes are thrown into vibration, the particular note emitted being due essentially to the length and tension of the latter. Thus, according to Garcia, in the production of the bass notes  the glottis is agitated

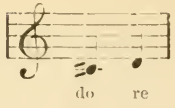
do, re, mi.

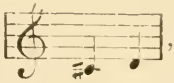
by large and loose vibrations throughout its entire extent, the lips comprehending in their length the anterior apophyses of the arytenoid cartilages and the vocal cords.

As the pitch of the sound rises through the gradual apposition of the apophyses the length of the glottis is encroached upon, and with the emission of the sounds  the apophyses touch each

si, do

other throughout their whole extent, their summits being solidly

fixed one against the other at the notes 

With the production of the notes  , and so on upward to the end of the register, the vibrations are due to the vocal membranes alone, the length of the glottis diminishing, and the cavity of the larynx becoming very small as the pitch of the voice continues rising. These changes undergone by the glottis in the shape and size and in the length and tension of the vocal membranes in the production of low and high notes by the larynx, as observed by Garcia and subsequent investigators, become intelligible when it is remembered, as shown in the last chapter, that the pitch of the note—that is, the number of vibrations per second—rises as the length of the string, pipe, or membrane diminishes, or the tension increases, the change in the shape of the glottis and of the tension of the vocal membranes being accomplished by the action of the muscles, as already explained. Thus, men have deeper voices than boys and women, their larynx being larger, and their vocal membranes longer. That the aperture of the glottis is narrowed during the production of sounds any one can convince himself by comparing the time of an ordinary expiration with that required for the passage of the same quantity of air during a vocal effort, and that the size of the aperture varies with the pitch of the note, from the fact of there being far less air expired during the production of a high note than in that of a low one. That the production of low and high notes is due to variations in the tension of the vocal membranes, as brought about by the action of the thyro-arytenoid and crico-thyroid muscles, is made evident during the passage of the voice from one extreme of the scale to the other by the movement of the thyroid on the cricoid cartilage, which is quite apparent if the tip of the finger be placed over the crico-thyroid ligament. As illustrating the nicety and precision with which the tension of the vocal membranes is regulated by muscular contraction, let us suppose, with Müller,[1] that the average length of the vocal membrane in man during repose is about $\frac{13}{100}$ of an inch, and during the greatest tension $\frac{9.3}{100}$, the difference being, therefore, $\frac{20}{100}$, or the $\frac{1}{5}$ of an inch, and that in the female the corresponding extremes are about $\frac{51}{100}$ and $\frac{63}{100}$, the difference being $\frac{12}{100}$, or the $\frac{1}{8}$ of an inch, and that the natural compass of the voice is about two octaves, or twenty-four semitones. Such being the case, as any cultivated voice can sing ten intervals between the twenty-four semitones, such a voice can produce 240 sounds, necessitating, however, over 240 different states of tension. Inasmuch, however, as the available length of vocal membrane to be tensed is only the $\frac{1}{5}$ and the $\frac{1}{8}$ of an inch in the sexes, it follows

[1] Op. cit., Vol. ii., p. 1018.

that in the production of each of the 240 sounds the vocal membrane must be diminished voluntarily by the $\frac{1}{1200}$ and the $\frac{1}{1920}$ of an inch in the case of the male and female singer, respectively, and by considerably less in the case of such phenomenal voices as those of Bastardella, Catalani, Cruvelli, and Patti, for example, with a compass of three octaves, and even more. The remarkable distinctness with which certain voices could be heard, like those of the celebrated basso, Lablache, and the late Madame Parepa Rosa, clearly above the sounds of a large chorus and orchestra, is due rather to the absolute accuracy with which the tension of the vocal membranes could be regulated by those great singers, to the purity of their tones rather than to the mere loudness or intensity. It should be mentioned, however, that the singers just referred to were of magnificent physique, as might have been expected, the power of the voice being due to the force with which the air is expelled from the lungs. As the action of the diaphragm and abdominal muscles has already been considered, it will be only necessary in this connection to recall what has already been said, that the inspiratory and expiratory acts can be so nicely balanced by a skilful singer as to enable him to produce the most delicate tones. It need hardly be added that while sounds may be uttered, and even words spoken during inspiration, that the true and natural voice, and, as we shall see presently, articulate speech are only produced during expiration. While, in childhood, the general character of the voice is the same in both sexes, in the adult condition the male voice differs very much from that of the female, the difference becoming marked at the age of puberty. If castration be performed, therefore, the contralto, or soprano, voice of the boy will be retained through life, and such a voice being susceptible of considerable cultivation advantage was cruelly taken of the fact at one time to fill choirs with desirable voices. After the age of puberty, however, the quality of the female voice remains the same, except in gaining strength and extending its compass. At this period, in the case of the male, however, the whole character of the voice changes through the development of the larynx. While the intensity of the voice in both sexes depends upon the force with which the air is expelled through the larynx, and the range or pitch, bass, tenor, contralto, and soprano, upon the length and tension of the vocal membranes, the quality of any particular individual voice, male or female, depends upon the shape, size, and general make of the larynx, and on the character of the auxiliary resonating cavities. In concluding our account of the production of the voice, a brief description, at least, of the influence exerted by the accessory vocal organs, viz., the trachea, ventricles, superior vocal cords, epiglottis, pharynx, nasal cavities, and mouth, should be offered. The trachea not only serves to conduct air to the larynx, but through the vibration of its own column of air reinforces the sound produced by the larynx, the vibration being perfectly appreciable if the finger be placed upon the

trachea during a powerful vocal effort. The ventricles probably, also, intensify the sound, the homologous parts being enormously developed in monkeys and apes possessing very loud voices, such as the South American howler (Myeetes), the chimpanzee, and gorilla.

That the superior or false vocal cords and the epiglottis are not essential to the production of the voice, can be shown by experiments like those of Longet,[1] in which the above parts were removed in animals without the voice being materially affected, and in man those cases in which the epiglottis had been lost through wounds or disease. The pharynx, mouth, and nasal fossæ, acting as resonating cavities, modify, however, very considerably the sounds produced by the vocal membranes. Indeed, in the production of the natural voice their resonance is essential. Thus, while in the production of low notes the velum palati is fixed, and the bucco-pharyngeal and naso-pharyngeal cavities reinforce the laryngeal sounds, in the passage upward to the higher notes these cavities are reduced in size, the isthmus contracting until, with the emission of the highest notes, the nasal fossæ is shut off entirely, and the mouth and pharynx alone resound, the tongue at the same time being drawn back into the mouth with its base projecting upward and the tip downward, the capacity of the resounding cavity is still further diminished. Such being the mechanism by which the chest tones or chest register are produced, it is only necessary to add, that if the velum palati be thrown forward instead of backward, thereby cutting off the mouth from the pharynx, the resonance being then due to the naso-pharyngeal cavity, that we pass from the chest register into that of the head tones or head register.[2] According to the late Madame Seiler,[3] however, the head tones are due to the vocal membranes being firmly approximated posteriorly, an oval opening being left with vibrating edges involving only one-half or one-third of the vocal membranes, which gradually contracts as the pitch of the tone rises. As in the case of the head register, so in that of the falsetto or middle register of the female, a difference of opinion still prevails as to the exact manner of its production. Thus, while, according to Fournié,[4] the falsetto is due to the tongue being pressed strongly backward and the epiglottis forced over the larynx; according to Seiler,[5] it is due to the thin, fine edges of the vocal membranes alone vibrating. While the distinction between the chest, falsetto, and head registers so far as pitch is concerned, is not an absolute one, and while we find that every voice possesses all three registers, nevertheless the chest register almost characterizes male voices and the contralto of the female, the falsetto being the most natural voice of the soprano, though the latter voice is capable

[1] Physiologie, Tome ii., p. 728. Paris, 1869.
[2] Fournié, Physiologie de la voix et de la parole, p. 421. Paris, 1866.
[3] The Voice in Singing, p. 56. Phila., 1868.
[4] Op. cit., p. 463.
[5] Op. cit., p. 56.

of chest tones, while the head voice is particularly well developed in tenors and in the female voice. The falsetto is but little cultivated at the present day by tenors, and even when it or either of the other two registers is particularly well developed the singer should endeavor to pass as insensibly as possible from one register to another, to give the impression that his voice possesses but one.

Speech.

While the position of man as the head of the animal kingdom depends upon the development of his intelligence, there can be no question that his superiority over all other animals is, to a great extent, due to his being able to convey his ideas to others by expression, or articulate speech.

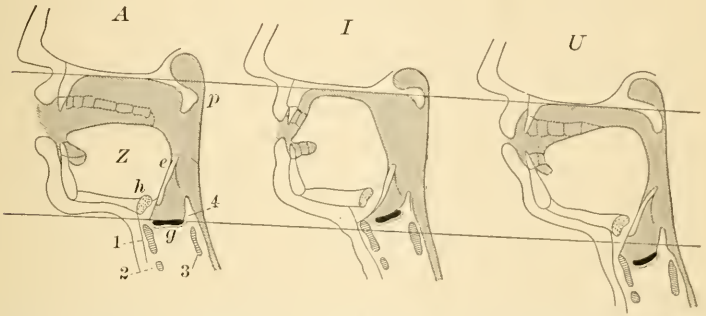
Speech is made up of syllables articulated or jointed together, the parts of speech called words being formed by the union of one or more syllables, the latter consisting usually of two kind of sounds, vowels and consonants.

Speech is voice modulated by the throat, nose, tongue, and lips. Voice may, therefore, exist without speech, and if the production of the voice be restricted to regular vibrations of the vocal membranes, it may be said that speech can exist without voice, since, in whispering, the vibrations of the muscular walls of the lips replace those of the vocal membranes, a whisper being, in fact, a very low whistle. Articulate sounds are usually divided by orthoëpists into vowels and consonants: vowels being continuous sounds due to the voice alone, but modified by the form of the aperture through which they pass out; consonants, interrupted sounds due to the interruption, more or less, of the voice, and sounded with vowels. This classification is not, however, a very natural one, since the sound of the English i, being a diphthongal sound, cannot be prolonged like a true vowel (a, o), while certain consonants (l, r, f) can be pronounced without the current of air being interrupted. The vowel sounds, by which we mean u, o, a, e, are due to the reinforcing of the overtones of the fundamental tone of the larynx by the cavity of the mouth, the changes in the shape of which give rise to so many resonators, each of which is adapted to the reinforcing of the particular overtone to which, together with the fundamental tone, the particular vowel is due. The presence of overtones coexisting with the fundamental tone of the larynx in the emission of vowel sounds, and the determination of what particular overtone accompanies the fundamental tone in the production of any particular vowel, can be shown by the Koenig manometric apparatus described in the last chapter.

Thus the vowel sound u is due to the fundamental tone being emitted strong, the cavity of the mouth or the vowel chamber (Fig. 502, *U*) being made as deep as possible, by keeping the tongue down at the bottom, and pushing the lips out, the mouth then reinforcing the fundamental tone of the larynx, and tuned, according to

Koenig[1] to the pitch of the note $Si\flat_2$ (Fig. 503), due to 224 vibrations per second. The sound o is due to the fundamental note of the larynx being present, but especially its first octave above being emitted also, and very strong, the cavity of the mouth being en-

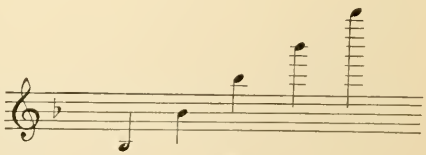
Fig. 502.



Section of the parts concerned in the formation of vowels. *Z.* Tongue. *p.* Soft palate. *e.* Epiglottis. *g.* Glottis. *h.* Hyoid bone. 1. Thyroid. 2, 3. Cricoid. 4. Arytenoid cartilage. (Landois.)

larged through the retraction of the lips so as to reinforce the octave, and tuned to the pitch of the note $Si\flat_3$, due to 448 vibrations per second. The sound a, like the preceding two vowels, is due to the presence of the fundamental tone of the larynx, but differs from o in that the fundamental is accompanied by the double octave above, the orifice of the mouth being so widened that the cavity of the mouth (Fig. 502, *A*) is tuned to the pitch of the note $Si\flat_4$ due to 896 vibrations per second. In the production of the sound e the cavity of the mouth is still more retracted, reinforcing the third octave above the fundamental, the cavity of the mouth being tuned to the pitch of the note $Si\flat_5$ due to 1,792 vibrations per second. As the four vowels u, o, a, e can be produced during one continuous expiration, during which the fundamental and overtones generated by the vocal membranes remain the same, by simply changing the shape of the mouth, it is evident that the production of each individual vowel will depend, as already mentioned, upon which particular octave or overtone is reinforced by the cavity of the mouth, the pitch of the latter depending upon its shape, and that the shape of the mouth remaining unchanged, the corresponding vowel will be emitted as long as the expiration blast lasts.

Fig. 503.



Vowels,	OU	O	A	E	I
Tones,	$Si\flat^2$	$Si\flat^3$	$Si\flat^4$	$Si\flat^5$	$Si\flat^6$
No. of Vibs.,	224,	448,	896,	1792,	3584.

Pitch of vowels. (Koenig.)

[1] Quelques : Experiences d'Acoustique, p. 65. Paris, 1882.

Now while the vowel i agrees with the four vowels just mentioned in being due to the reinforcement of an overtone, the fourth octave accompanying the fundamental by the cavity of the mouth (Fig. 502, *I*), which in this instance is tuned to the pitch of the note $Si\flat_6$, due to 3,584 vibrations per second, an octave higher than in the case of the vowel e, it differs from the true vowels in that, the cavity of the mouth remaining the same, if the expiratory blast be prolonged, it does not remain i, but becomes e. The vowels are the only real vocal sounds, it being only on a vowel that a note can be said or sung. Speech, however, is made up not only of vowels, but of consonants—that is, of sounds that are sounded in conjunction with a vowel. While the distinction between vowels and consonants, as already mentioned, is not an absolute one, it may be said that while vowels are due to the vibrations of the vocal membranes being modified by the mouth, consonants are due to the expiratory blast being interrupted in various ways in its course through the throat and mouth; the vibrations of the vocal membranes, when essential, being rather secondary in character. Consonants may be divided, according to their manner of production, into two kinds, explosive and continuous, the sound of the explosive consonants being due to the sudden establishment or removal of a particular interruption, that of the continuous consonant to the air rushing continuously through some constriction, for example, explosive consonants are the labials p, b, dentals t, d, and gutturals k, g, p, t, and k, being uttered without the voice, the so-called surds b, d, and g (hard) with the voice sonants—that is, are accompanied by a vowel sound. In uttering p the lips are first closed, then the expiratory blast suddenly opening them, the sound is produced. Similarly the sudden interruption of the contact of the tip of the tongue with the hard palate, and of the root of the tongue with the soft palate gives rise respectively to the sounds t and k. The continuous consonants are subdivided into aspirates, resonants, and vibratory.

In certain cases a brief sound due to the sudden opening of the closed glottis, the so-called spirited lenis, inaugurates a vowel, the vibrations of the vocal membranes immediately following with the production of a true vowel sound. In other cases in uttering a vowel the glottis being open but constricted irregular vibrations produced by friction give rise to the so-called spiritus aspera.

The aspirates include the labials f, v, the dentals s, l, sh, th (hard), z, zh, th (soft), and the gutturals ch, gh. Like the explosive consonants, some of the aspirates are uttered without the voice, as f, s, l, sh, c, h; some with the voice, as v, z, zh, th, ch. The resonants include the sounds m, n, ng, and the vibratory the sound r, common and guttural. Of the aspirates, f and s are formed through the lips and teeth being brought nearly in contact respectively; th through the placing of the tongue between the two partially open rows of teeth; l when the tip of the tongue is placed

against the hard palate, and the air escapes at the sides; sh through the dorsal surface of the tongue being raised toward the palati, the passage-way between the two being thereby narrowed; ch and gh through the approximation of the root of the tongue to the soft palate. In the production of all of the resonants the vocal membranes vibrate and the nasal chambers resonate, the closing of the lips in particular giving rise to m, the contact of the tongue with the hard palate to n, and the approximation of the root of the tongue to the soft palate to ng. The vibratory consonants include the various forms of the sound r, so called on account of being produced by the vibration of the constricted portion of the vocal passage; thus, the common r is due to the vibrations of the point of the tongue elevated against the hard palate; the guttural r to vibrations of the uvula or other parts of the walls of the pharynx. The tongue, while an organ of speech, is not essential, since after its loss the faculty of speech, more or less perfect, remains. Finally, while the consonant e is a breathed aspirate, it differs from all other letters in being formed in the larynx itself, the glottis being narrowed enough to produce a wind-rush, but not sufficiently to throw the vocal membranes into vibration. c is redundant, producing the same effect as k or s; q is equivalent to l, being used only before the vowel u; x is the same as ks at the end of a syllable, and z when beginning a word.

While the limits of this work will not permit of any further detailed consideration of orthoëpy, or of any theory of the origin and growth of language in general, or of that of the language in which this work is written in particular, the above description will suffice as a general account of the production of articulate speech, a factor almost as important as that of intelligence in the development of civilization.

CHAPTER XLIII.

THE STRUCTURE OF THE EAR, AND THE SENSATION OF HEARING.

The organ of hearing is usually described as consisting of three parts, the external ear, including the pinna or auricle and the external auditory meatus, the middle ear or tympanum, and the internal ear, including the labyrinth and the auditory nerve. For convenience, as well as to avoid repetition, the functions of the three parts of the ear will be considered at the same time as that of the description of their structure.

The Structure and Functions of the External Ear.

The pinna, auricle, or ear, in the ordinary sense of the term—that is, the portion projecting from the head (Fig. 504), with the excep-

Fig. 504.

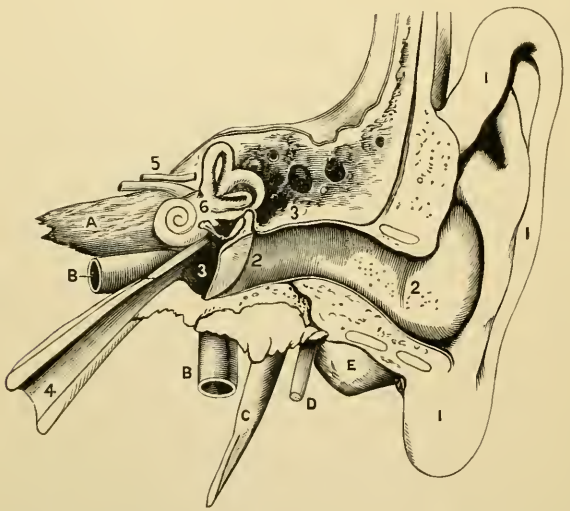


Diagram of organ of hearing of left side. 1. The pinna. 2. Bottom of concha. 2, 2. Meatus externus. 3. Tympanum. Above 3, the chain of ossicles. 3. Opening into the mastoid cells. 4. Eustachian tube. 5. Meatus internus, containing the facial (uppermost) and auditory nerves, 6, placed on the vestibule of the labyrinth above the fenestra ovalis. A. Apex of the petrous bone. B. Internal carotid artery. C. Styloid process. D. Facial nerve, issuing from the stylo-mastoid foramen. E. Mastoid process. F. Squamous part of the bone. (Quain after Arnold.)

tion of the lower lobular portion, consists of fibro-cartilage and presents certain prominences, the tragus and antitragus ridges, the helix and antihelix, which, together with their fossæ, adapt it to receive the aërial vibrations giving rise when transmitted to the auditory

nerve to the sensation of sound. Owing to the immobility of the ear, through the imperfect development of the attolens, attrahens, and retrahens auri, as well as its intrinsic muscles, the external ear is not as functionally important in man as in the case of the lower animals for the appreciation of the intensity of sound, since persons deprived of it do not experience any sensible change in their power of hearing. That the auricle is, however, of use in enabling us to judge as to the direction of sounds, any one can convince himself by filling the convolutions with wax, or flattening the ear forcibly against the side of the head, when it will be found impossible to determine the direction from which the sound comes. Such is also the experience of those persons who have lost the external ear from wounds, etc. Indeed, there can be little doubt that we judge as to the origin and direction of sounds from the fact that the sound waves do not impinge upon the ears alike, and that the intensity of the sound is modified by the manner in which it falls upon the external ear and is reflected from it. Hence, in determining whether a sound proceeds from directly behind or in front of us, we usually incline the head in the direction from which we suppose it to come. The aërial vibrations having been collected by the auricle, are thence transmitted by the external auditory meatus from the concha or the deep concavity within the position of the antihelix and subdivided by the helix to the tympanum. The external auditory meatus, about an inch and a quarter in length, is directed inward and forward, upward and downward, and is narrowest at its middle portion. It consists of two portions, an interfibro-cartilaginous one, the prolongation of the auricle, and an inner osseous one, a part of the temporal bone, both portions being lined with skin. The skin of the outer portion is thick and provided with numerous hair, sebaceous and ceruminous glands. The latter, small, round, brownish-yellow bodies imbedded in the subcutaneous tissue, and giving rise to the punctured appearance of the skin, are modified sudoriferous glands, consisting, like the latter, of a narrow tube coiled upon itself in the form of a ball, and secrete the cerumen or ear-wax. The latter is said to be composed of fatty and albuminous matters of salts of soda and lime, and has a very bitter taste, a property which has been considered of service in preventing insects entering the ear. The cerumen, which probably consists of sebaceous matter mixed with the proper secretion of the ceruminous glands, lubricates the meatus. The skin of the inner osseous portion of the meatus is very thin, destitute of hairs and glands, and at the bottom of the meatus is continued over the tympanic membrane as its outer investing layer.

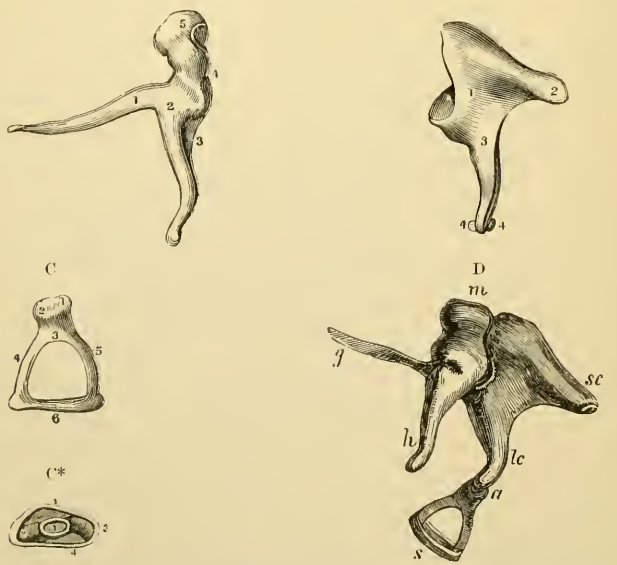
The Structure of the Middle Ear.

The middle ear, separated from the external ear by the tympanic membrane, includes the tympanum or drum of the ear, the ear bones, with their ligaments, muscles, the mastoid sinuses, and the Eusta-

chian tube. The tympanum, an irregular cavity in the interior of the petrous portion of the temporal bone, is about half an inch in height and breadth, and perhaps the sixth of an inch from without inward, is closed in front by the tympanic membrane, at the back by the wall of the labyrinth, and opens above and posteriorly into the sinuses and in front into the Eustachian tube. The tympanic membrane separating, as already mentioned, the external auditory meatus from the tympanum, is about two-fifths of an inch in height and breadth, somewhat funnel-shaped in form, and is disposed obliquely, making an angle of 40° with the floor of the meatus. That part of the membrane drawn inward by the tip of the manubrium of the malleus and constituting a central depression is called the umbo. The oblique position of the tympanic membrane is of advantage, since more sound waves fall vertically upon it than if it were placed vertically.

The tympanic membrane is inserted by the greater part of its circumference into a groove which, while in the adult is regarded as a portion of the temporal bone, is in reality the only part visible of an originally entirely separate osseous ring, the homologue of the

FIG. 505.



Bones of the tympanum of the left side. A. Malleus. 1. Long or slender process. 3. The handle. 4. Short process. 5. Head. B. Incus. 1. Body. 2. Short or posterior process. 3. The long process with the orbicular process 4. C. Stapes. 1. Head. 4, 5. Crura. 6. Base. D. The three bones in their natural connection. *m.* Malleus. *sc.* incus. *s.* Stapes. C*. Base of the stapes.

tympanic bone of the lower vertebrates, but which in man, instead of remaining distinct as in them, coössifies as development advances with the temporal bone, and grows outwardly as the osseous external auditory meatus, its morphological significance being thereby entirely lost sight of.

At the point where the ring of bone is wanting the tympanic membrane is attached to the bone above, and being less tense in that position even when thrown into folds is distinguished as the membrana flaccida. The tympanic membrane, thin and translucent, is composed of a layer of fibrous tissue, the membrana propria, covered externally by the skin of the external auditory meatus, and internally by the mucous membrane of the tympanum, the latter being continuous with that lining the Eustachian tube. The fibrous layer of the tympanum consists of two sets of fibers, of which the greater part radiate from its center, the remaining ones being concentrically disposed at the periphery. The little ear bones (Fig. 505), three in number, the malleus, incus, and stapes, are disposed within the tympanum from before backward in the order named. The malleus, so called on account of its resemblance to a hammer, is suspended vertically from the floor of the tympanum by a slender band of fibers, the suspensory ligament, which passes into its head, the latter articulates through an oval facet covered with cartilage with the body of the incus. The malleus is also connected with the tympanic membrane, its tapering, slightly twisted manubrium or handle passing down into the fibrous layer of the latter as far as its center. From the neck of the malleus, or the constricted portion below the head, two processes are given off.

The larger process or processus gracilis projecting at right angles and passing into the Glasserian fissure is attached by ligament to the spinous process of the sphenoid bone. The smaller process gives attachment to the tensor tympani muscle, so called on account of its tensing the tympanic membrane and which, arising from the end of the cartilage of the Eustachian tube, and the contiguous surfaces of the sphenoid and temporal bones, passes through a special canal of the latter into the tympanum.

The incus or anvil, situated behind and articulated with the malleus as already mentioned, is also sustained in its position by a fibrous band, passing from its short process to the margin of the opening leading into the mastoid cell. The long process of the incus, curved and tapering, descending nearly parallel with the manubrium or handle of the malleus, terminates in the so-called orbicular process, by which it articulates through cartilage with the facet on the head of the stapes, or stirrup. The orbicular process is in reality a distinct bone, being separable from the incus even at birth; soon after, however, it becomes so ossified with the latter as to be undistinguishable from it. The stapes, or stirrup, situated inwardly between the incus and the foramen ovale of the vestibule, is disposed at right angles to the long process of the incus, the crura—that is, the portion joining its head and its base, lying horizontally in the tympanum. By its annular ligament, the margin of the base of the stapes is connected with the border of the foramen ovale of the vestibule, the pressure of the base of the stapes against the oval window or the perilymph back of it being regu-

lated by the stapedius muscle, which, arising within the hollow of the pyramid, or the conical eminence projecting from the back part of the tympanum, is inserted into the head of the stirrup.

The mastoid sinuses, so called from being situated in the interior of the mastoid portion of the temporal bone, are irregular cavities lined with mucous membrane, which communicate by a large orifice with the upper and back part of the tympanum. The Eustachian tube (Fig. 504, *e*), about an inch and a half long and somewhat trumpet-shaped in form, extends from the front part of the tympanum obliquely downward, forward, and inward, terminating by an oval orifice in the pharynx on a level with the turbinated bone at the back of the posterior nasal orifice. The Eustachian tube consists of two portions, an upper osseous portion situated in the petrous portion of the temporal bone and opening into the tympanum, and a lower fibro-cartilaginous portion opening into the pharynx, the two portions being united within the angle between the squamous and petrous portions of the temporal bone. It is lined with mucous membrane provided with ciliated epithelium, continuous on the one hand with that of the tympanum, and on the other with that of the pharynx. The existence of such a tube as that just described, putting the cavities of the middle ear in communication with that of the pharynx, as well as the presence of a chain of bones connecting the membrana tympani with the oval window of the vestibule, will become intelligible when the development of the ear is considered.

Functions of the Middle Ear.

Such being in general the structure and relations of the tympanic membrane, ear bones, Eustachian tube, etc., if the aërial vibrations collected and transmitted by the auricle to the external auditory meatus throw the tympanic membrane into vibration, the vibrations of the latter will in turn be transmitted by the ear bones through the intermediation of the fluids of the vestibule, etc., to the terminal filaments of the auditory nerve, and so give rise to the sensation of sound.

The importance of the membrana tympani in audition is shown by the fact that the acuteness of hearing is always more or less affected in those cases in which the membrane is thickened, perforated, or destroyed, and that relief is obtained by the wearing of an artificial membrane if the latter can be tolerated. This becomes perfectly intelligible when it is remembered, as shown by Müller,[1] that while aërial vibrations are communicated to solid bodies like the ear bones only with difficulty and with considerable diminution in their intensity, they are communicated very readily to the same, a tense membrane like the tympanic membrane intervening, the fact of the membrane being fixed at the periphery, and having air on both sides of it being also most favorable conditions. That mem-

[1] Physiology, Vol. ii., p. 1248.

branes of as small extent as that of the membrana tympani when stretched are readily thrown into vibration, can be shown by experiments like those of Savart[1] in which sand strewed over their surface was cast off, on sonorous vibrations being excited in their vicinity. It is a well-known fact, that membranes vibrate more powerfully, more intensely, when relaxed than when tensed, hence the sensitiveness to all sounds experienced in facial palsy, which is due to the want of innervation of the tensor tympanic muscles by the filaments of the paralyzed facial supplying it. It is also worthy of mention in this connection that the vibrations of the membrana tympani are more intense in proportion as the latter approaches a vertical position, as accounting to some extent for the appreciation of sounds by musicians, in some of whom the tympanic membrane is almost vertically disposed, whereas in persons with but little ear for music the membrane is very oblique in position. It has already been explained that sounds not only differ in their loudness or intensity, but in their pitch or number of vibrations per second as well, and since we hear sounds of different pitch, it is obvious, therefore, that there must be some means of tuning—that is, of tightening or relaxing the tympanic membrane, so that the vibrations of the latter shall be the same per second as those to which the particular note or notes heard are due. That is to say, every sonorous aërial wave—that is, a condensation and a rarefaction—bending the tympanic membrane once in and once out, the rate of vibration of the membrane must be the same as that of the vibration of the sonorous body causing it, if the particular sound due to the latter is to be heard. That the membrana tympani is relaxed for sounds of low pitch and tensed for those of high pitch. is shown by the insensibility to low tones, and marked appreciation to high ones, being proportional to the extent to which the membrane is tensed. Thus, if the mouth and nose being closed, we attempt to breathe forcibly by expanding the chest, the air within the tympanum becoming rarefied, the tympanic membrane will be forced in by the external air and rendered more tense, the effect of which is that, as Dr. Wollaston[2] showed, we become deaf to low sounds. A similar deafness to sounds of low pitch is also produced, the nose and mouth being stopped when a strong effort is made to expire, the increased tension of the membrane being due, however, in this instance to the air being forced into the tympanum through the Eustachian tube instead of being sucked out of it and the membrane being pushed outwardly. A sudden concussion may produce temporary deafness in either of the above ways—that is, by forcing air either into or out of the tympanum.

It is evident, from the facts just mentioned, that the function of the Eustachian tube is the maintaining of equilibrium between the air within the tympanum and the air without. Hence if the tube

[1] Journal de Physiologie, Tome iv., p. 203. Paris, 1824.
[2] Philos. Trans., Lond., 1820, p. 306.

be closed, which is usually the case, according as the external air becomes denser, as in descending in a diving-glass, or rarer, as in making high mountain ascents, the tympanic membrane will be pushed in or out in either case, will be rendered more tense and pain and deafness experienced, both of which can, however, be usually relieved by the act of swallowing, which, in opening the Eustachian tube, reëstablishes the equilibrium between the internal and external pressure. It may be mentioned, in this connection, that the Eustachian tube is opened by the contraction of the tensor palati, levator palati, and the palato-pharyngeus muscles; the tensor palati, in drawing the hook of the cartilage outward, and the levator palati, in drawing the end of the cartilage upward and inward, enlarge and widen its pharyngeal orifice, the palato-pharyngeus fixing the cartilage. With the relaxing of the muscles just mentioned, through the elasticity of the cartilage, the tube then closes again almost entirely, a narrow chink alone remaining. Since, while the Eustachian tube is open, the cavity of the tympanum is in communication with that of the pharynx, it follows that if we swallow several times in succession, the nose and mouth being closed, that the air will be gradually drawn from the tympanic cavity, the membrane being rendered tense by the external atmospheric pressure, as in the case just mentioned, in which forced inspiratory efforts were made, and an insensibility to low sounds experienced. That the tympanic membrane is tensed for high sounds is shown by the fact that in certain individuals,[1] whose ordinary limit of appreciation was of sounds due to fifteen hundred vibrations per second by voluntary contraction of the tensor tympani muscle, this was increased, so that sounds could be heard due to 2,500 vibrations per second. There can be little doubt, then, that the membrana tympani is relaxed or tensed, according as the sonorous vibrations are low or high in pitch, and that the variations in the tension of the membrane are regulated by the action of the tensor tympani muscle. While there is a great difference in individuals as regards the appreciation of sounds, some persons being insensible to the hum of insects, the chirrup of the sparrow, the squeak of the bat, others to the high sounds of small organ-pipes, or even the highest notes of the piano, there is a limit, nevertheless, to audibility in all, the tympanic membrane failing to link together into a continuous tone vibrations succeeding each other less rapidly than 16 a second, or more so than 38,000 a second. In the former case, we are conscious only of separate shocks; in the latter, we are unconscious of sound altogether. The range of audibility lying within the above limits embraces, therefore, about 11 octaves, of which about two-thirds, or 7 octaves only, are, however, made use of in music. It is true that we obtain from the lowest C of the piano the note due to 32 vibrations per second, and from the lowest A of the new grand piano that due to 27 vibrations per second, and from a

[1] Blake, Trans. of the Amer. Otological Soc., Vol. v., p. 77. Boston, 1872.

closed organ-pipe 16 feet long, or an open one 32 feet long, the lowest C, due to 16 vibrations per second, but the latter sound, and that of the lowest C or A of the piano, are so unmusical, so dull and groaning in character, that they are but little used. The deepest tone made use of in orchestral music being that due to the E string of the double bass, giving 41¼ vibrations, the highest that of the D of the piccolo flute, due to 4,752 vibrations per second; it may be said that practically the range of musical sounds is confined between 40 and 4,000 vibrations per second, the highest C of the piano reaching 4,224 vibrations per second—that is, in round numbers, as just said, about 7 octaves. Even within such limits the immense number and kind of sonorous waves that fall upon the tympanic membrane while listening to a grand opera as given by the leading artists, together with full choral and grand orchestral accompaniment, must impress one with the remarkable acoustic properities of the membrana tympani, so small and delicate, and yet so susceptible to such an immense number and variety of sounds. But little imagination is required to picture to one's self, during the performance of an opera, the sonorous waves flowing across the auditorium, and breaking upon the drum of the ear like those of the ocean upon some weather-beaten rock or beach, the long waves, from 35 to 12 feet in length proceeding from the deep bass instruments and voices of the bassos like billows from the distant sea, the short ones from 30.3 inches in length, like ripples or white caps, from the violins, flutes, and voices of the tenors and sopranos, with intermediate ones of different lengths, and yet all following each other in such orderly mathematical sequence that, amidst such a variety of sounds, we are conscious of nothing but melodious and harmonious tones. From the fact of our being able to appreciate the latter, it is obvious that the tympanic membrane is susceptible of being impressed by simultaneous as well as by successive sounds, and while the limits of this work do not permit of any consideration of harmony, discord, of chords, of consonant intervals, or those that give the ear a sense of relief, or dissonant ones that must be resolved, etc., it seems proper to point out and illustrate the fact that the vibrations to which harmonious sounds are due are in a definite ratio to each other, and, that, whatever the cause may be, sounds are harmonious in proportion as the ratio between the number of the vibrations giving rise to them is a simple one.

The simplest ratio being one to one, two sounds, as produced by the siren, for example, will be in perfect union, if the pitch of both be the same. The next simplest ratio being 1 to 2, a harmonious sound will remain, if with the fundamental its first overtone above, or octave, be at the same time given—that is, if with Do^3 C^3 256 vibrations per second, Do^4, C^4 512 vibrations per second be also sounded. The waves, never interfering with each other, will give rise to no discord, and the two sounds blended into one may be continued indefinitely. Proceeding in the same manner, according

to the simplicity of the ratio, the next in order will be that of 2 to 3, or C to G—that is, with Do^3 C^3 256 vibrations per second, Sol^3 G^3 384 vibrations per second may be sounded; for there being for every two waves of C three waves of G, there will be a coincidence for every second wave of C and every third wave of G. The next ratio being that of 3 to 4, or C and F, C^3 and F^3 Fa^3, 341.3 vibrations per second, may be sounded together. Although we have already shown by the siren that the sounding of the notes C E G, together, give rise to the harmonious major chord, nevertheless, according to the law that the smaller the ratio of vibration between different sounds the more perfect the harmony, the combination of C with E—that is, in the ratio of 4 to 5, or, as in the above, of 256 to 320—is a less pleasing one than that of C to F, in which the ratio is 3 to 4. It is the want of harmony of F with G that excludes it from the cord C E G C; the cord C F A C is, however, a harmonious one. Continuing the next ratio, that of 6 to 5, or of C to E flat, a minor third, consistently with its ratio, being less simple than that obtaining in the major third, is a less harmonious one. Finally, as illustrating a step further the law just enumerated, it may be mentioned, though well known, that the interval corresponding to a tone in which the vibrations giving rise to the two notes C^3 D^3, for example, are in the ratio 8 to 9, 256 to 288 is a dissonant one, and that the interval of a semitone C to D flat, in which the ratio is 15 to 16, is a very sharp, grating, and dissonant one. About five hundred years before our era[1] it was shown by Pythagoras that if a stretched string was so divided into two parts that one was twice the length of the other, and the two parts of the string sounded simultaneously, that the note emitted by the short part was the octave emitted by the long one. Continuing to experiment, this celebrated philosopher next showed that if the string be divided in the ratio of 2 to 3 then the interval between the notes emitted would be that of a fifth; and further, that, according to the ratio in which the string was divided, the remaining more or less consonant intervals would be heard, the harmony of the two sounds being proportional to the simplicity of the ratio of the two parts into which the string was divided.

	1st.	2d.	3d.	4th.	5th.	6th.	7th.	8th.
Note, ...	C	D	E	F	G	A	B	C
Lengths of the string,	1	$\frac{8}{9}$	$\frac{4}{5}$	$\frac{3}{4}$	$\frac{2}{3}$	$\frac{3}{5}$	$\frac{8}{15}$	$\frac{1}{2}$
Number of vibrations,	256	288	320	341	384	426	480	512

This important law, the first step made in the physical explanation of musical intervals, Pythagoras, however, did not account for, it remaining for later investigators to show that the vibrations of strings are inversely proportional to their length. It has just been mentioned that while the combination of a fundamental tone with its octave, for example, is a consonant, pleasing one, giving

[1] Montucla, Hist. des Mathematiques, Paris, An. vii., Tome i., p. 114.

rise to no discord, that of the interval of a tone, or of a semitone, is a dissonant, disagreeable, discordant one. It remains for us now, therefore, to determine, if possible, the physical cause of discord. It will be remembered that in the double siren of Helmholtz there are two series of 12 orifices, each common to both sirens; such being the case, if both these series of orifices are opened and air forced through the instrument, the two sounds produced will be in unison, and will continue so, since the pitch of both will be the same however low or high the sound may be. In describing the double siren attention was also called to the fact that, by turning the handle of the upper siren the orifices of the wind chest will either meet or retreat from those of its retreating disk, the pitch of the upper siren rising or falling accordingly. But the relation of the rotation of the handle to that of the upper wind chest is such that if the handle be turned through 45 degrees the wind chest turns through 15 degrees, or through the $\frac{1}{24}$ of its circumference, which causes the orifices of the upper wind chest to be closed at exactly the same moment that the 12 orifices of the lower wind chest are opened, and *vice versâ*, the effect of which is that the intervals between the puffs of the lower siren—that is, the rarefactions of its sonorous waves—will be filled up by the puffs or condensations of the waves of the upper one. But if the condensation of the one set of sonorous waves coincides with the rarefactions of the other set there will be neither condensation nor rarefaction, upon which all sound depends, the fundamental sounds of the siren will be extinguished through the interference of the two sounds, as it is called, and absolute silence would result were it not for the presence of the overtones of the siren. Rotating, however, the wind chest through 30 degrees, or the $\frac{1}{12}$ of its circumference, by turning the handle through 90 degrees, the puffs or condensations of the sonorous waves of the lower siren will coincide with those of the upper one, reinforcing the latter; and as this latter takes place once for each 90 degrees, there will be 4 of these reinforcings, or beats, as they are called, for every 360 degrees, or for one rotation of the handle.

The change in the pitch of the sound emitted by the upper siren induced by the rotating of the handle, the pitch of the sound emitted by the lower siren remaining the same, gives rise then to beats, of which there will be four for every one rotation of the handle. For a time, however, there may be heard twelve or eight beats; when such is the case, it is due to the strength of the second or first overtone being sufficient to overpower the fundamental, which vibrating three times and twice as rapidly as the fundamental, will, of course, give rise to three times, or twice as many beats. It is through the presence of these overtones that, though the tone of the fundamental may swell or sink as the handle is turned, sound is still heard, even though the handle reach the position at which the fundamental sound through interference is extinguished. Beats

can be readily produced by tuning forks which are especially suited for this purpose, no overtones being generated if the forks be properly toned. Let us suppose, for example, that of two standard tuning forks Do^3, each giving 256 vibrations per second, and whose sounds are therefore in unison, one of which be weighted just sufficiently to cause it to vibrate a little more slowly than the other, say 255 times. The two sounds then emitted will no longer flow on continuously in unison, there being now alternate diminutions and reinforcements of the sounds or beats, and in this particular case one beat per second, which, it will be observed, is exactly the difference between the two rates of vibration of the two forks, 256 and 255. A moment's reflection will make it clear why the beats should occur, and at such a rate. Since the one fork vibrates 256 times in a second, and the other 255 times, it is evident that at the end of the second the wave of the latter fork will be one vibration behind that of the former, and at the end of a half second a half a wave behind, the one fork having made 128 vibrations, the other $127\frac{1}{2}$, but at that moment the condensation of the one wave coinciding with the rarefaction of the other, the sounds will be extinguished through their complete interference with each other. From the half of the second onward, however, until the end of the second, the condensations reinforce each other more and more, until at the end of the 256th vibration of the one fork, and the 255th of the other, condensation coincides with condensation, and rarefaction with rarefaction, the full effect of both sounds being then experienced. Similarly, from the half second where the interference is complete backward to the beginning of the second, condensation coincides more and more with condensation, rarefaction with rarefaction, until at the beginning of the second, of course, as at the end, the coincidence is complete. Suppose, however, that the two forks vibrate 240 and 234 times a second, then at the end of the first $\frac{1}{6}$ of a second, one fork will have generated 40 sonorous waves, the other 39, the one wave being one vibration ahead of the other, and therefore, at the end of the $\frac{1}{12}$ of a second, half a vibration ahead. This instant being, however, that at which interference is complete, during which the sound is extinguished, the time elapsing on the one hand between it, or the $\frac{1}{12}$ of the second, and the beginning of the second, and on the other to the end of the $\frac{1}{6}$ of the second, will be characterized, as in the preceding case, by a gradual diminution, followed by a gradual augmentation of the sound or one beat; but as this is repeated in this case six times during the second, there will be six beats, which, it will be observed, is exactly the difference between the two rates of the forks, 240 and 234. Experimenting this way with forks, pipes, etc., it can be proved that the number of beats per second is always equal to the difference between the rates of vibration of the two sounds to whose interference they are due. Now it has been shown by Helmholtz that if the beats per second succeed each other less rapidly than 33 per second, the sound is not

disagreeable, but if at that rate, the dissonance becomes then absolutely intolerable. As the number of beats per second, however, increases, the dissonance diminishes, and when the beats have reached the rate of 132 a second, they disappear and discord vanishes. Beats are therefore the cause of dissonance or discord, and intervals free from them will be harmonious. Thus the fundamental, due, for example, to 256 vibrations per second, when continued with its octave to 512 vibrations is a harmonious one, free from beats, since the difference in the rate of vibration, or 256, is too high to admit of them. The interval of the fifth C and G is still harmonious, the difference in the rate of vibration, $384 - 256 = 128$, being also too high. On the other hand, the interval of the fourth C and F due to 341 and 256 vibrations per second respectively, is somewhat dissonant, the difference between the rates of vibration being 59, admitting, therefore of that number of beats below the limits at which discord vanishes; and the interval of C and E more dissonant still, the difference in their rates of vibration being 64, the notes being due to 256 and 320 vibrations per second, respectively. It should be mentioned in this connection, in order to avoid any misconception, that the phenomenon of beats is of an entirely different nature from that of the resultant tones discovered by Sorge, Tartini, and Helmholtz. That resultant tones should ever have been considered as identical with beats, is not so strange, since the rate of vibration of the first difference tone, or the loudest resultant tones like that of beats, is equal to the difference in the rates of vibrations of the two primary sounds producing them, which led the celebrated Young to regard resultant tones as due to the linking together of rapidly recurring beats. That a resultant tone is not made up of beats is shown by the fact that while a resultant tone due to thirty-three vibrations per second is smooth, consonant, musical beats succeeding each other at that rate, as already mentioned, are most dissonant.

In concluding this necessary digression upon the nature of musical intervals, discords, beats, resultant tones, etc., it must be observed that whether they are caused in the manner indicated, or however they may be accounted for physically, hereafter, in any case, no explanation whatever is offered why one rate of vibration should affect us agreeably, and another rate disagreeably—that is, if sounds are harmonious through the absence of discords, why should the presence of the latter give rise in us to a sense of discomfort, dissonance? Nor have we any reason to hope, judging from the past, that the study of mere acoustics will ever throw any light upon our sensations of tone subjectively, or contribute to the progress of music objectively. Indeed, it appears to be generally forgotten by the cultivators of harmony that the best music was composed when acoustics was in its infancy, to this day, the best illustration of theoretical harmony being taken from the works of Mozart, Handel, Haydn, the science of sound having not added one cord or progression that was not known to Bach.

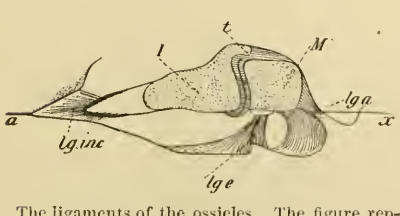
Remarkable as are the properties of the tympanic membrane, and essential as it is undoubtedly in normal hearing, when it is remembered that it, together with the remaining part of the middle as well as the external ear, is only the intermediate means by which the terminal filaments of the auditory nerve are excited, it becomes intelligible why after the rupture or even absence of both membranes, hearing, though impaired, and appreciation of musical sounds are still possible.

The innumerable and different kind of sonorous waves impinging upon the tympanic membrane and throwing it into vibration to be appreciated in consciousness as sounds, must be thence conducted to the vestibule of the internal ear. This is accomplished by the chain of ear bones stretching across the tympanum from the tympanic membrane to the foramen ovale of the vestibule. The ear bones, while three in number, in point of fact may be regarded physiologically as being equivalent to one long bone, vibrating to and fro with the tympanic membrane. That such is the case is not only shown by the manner in which the bones are articulated with each other, but from the fact that in the lower vertebrates the homologue of the stapes is a long rod-like bone, passing from the tympanic membrane to the vestibule, while the homologues of the incus and malleus are not situated within the tympanum, but outside of it, entering into the formation of the lower jaw.

Movements of the Ear Bones.

The articulation of the malleus and incus is such that while with the outward movement of the manubrium of the malleus, the head of the latter moves freely in the joint, with the inward movement of the latter the malleus and incus move together as one bone, the lower projecting margins of their articulating surfaces interlocking together like the teeth of a Bregnet watch key.[1] The malleus and incus move freely about an axis (*a x*, Fig. 506) one end of which passes through the anterior ligament of the malleus, the other end through the ligament of the incus.

Fig. 506.



The ligaments of the ossicles. The figure represents a nearly horizontal section of the tympanum, carried through the head of the malleus and incus. *M.* Malleus. *I.* Incus. *t.* Articular tooth of incus. *lga*, Anterior and *lge* External ligament of the malleus. *lg inc.* Ligament of the incus. The line *ax* represents the axis of rotation of the two ossicles. (Hensen.)

In the case of audition, as in that of vision, the sensation lasts longer than the stimulus. Hence, when the interval of time elapsing between two sounds such as that of a pendulum beating seconds is less than the $\frac{1}{100}$ of a second, the sensations of the two sounds are fused into one sensation. The ear, like the eye, experiences also fatigue.

[1] Helmholtz, Sensations of Tone, trans. by Ellis, 1875, p. 196.

Thus, for example, when the sound of a tuning fork becomes inaudible to one ear, if the fork be placed to the opposite ear, the sound will be heard distinctly. It is due to the ear becoming fatigued that a person who has been listening for some time to a particular overtone fails to hear the same when the latter is sounded with its fundamental and the accompanying series of overtones. The note sounded under such circumstances seems to be poor in quality. Difference of opinion still prevails as to the number of vibrations that must fall upon the ear to give rise to the consciousness of sound. According to some from two to five vibrations per second will cause a sensation of sound, a greater number of vibrations being, however, necessary, as we have seen, to produce in consciousness the sensation of a distinct musical note. In audition, as in the case of the other senses, there is a minimum stimulus necessary for the production of sound. It is said that a pith ball weighing one milligramme (0.0154 grain) falling through 1 mm. ($\frac{1}{25}$ of an inch) upon a glass plate will be heard at a distance of 91 mm. (3.6 inches). The "constant proportion," that is the increment necessary to cause the sensation of sound, is said to be, as in the case of the sensation of touch, temperature, one-third of the original stimulus. In inward movements of the tympanic membrane the three ear bones move as one bone around the axis of suspension, the maximum amplitude of the center of the tympanic membrane being from the $\frac{1}{12}$ to $\frac{1}{9}$ mm., that of the stapes, however, only from the $\frac{1}{18}$ to $\frac{1}{14}$ mm. That the stapes is pressed against the liquid of the vestibule by the movement of the tympanic membrane and ear bones can be shown experimentally, as by Helmholtz, by fitting a slender glass tube into the semicircular canal and filling the vestibule and part of the tube with water, when, through the forcing of the tympanic membrane inward, the water will be seen to rise nearly a millimeter ($\frac{1}{25}$ of an inch).

In outer movements of the tympanic membrane, while ordinarily the articulating processes appear to be retained in apposition by the elastic reaction of the ligament and the stapedial attachment of the incus, in cases where the tympanic membrane is abnormally forced outward the malleus leaves the incus behind, alone completing its outward motion. By this provision of nature the stapes escapes being torn out of the oval window.

The movement upon the tympanic membrane and ear bones can be graphically studied and recorded, as by Koenig,[1] by attaching a style to the incus or malleus, the tympanic membrane being thrown into vibration by two organ-pipes, and the sound of the latter reinforced by a resonator.

Inasmuch as the distance from the tip of the manubrium, where the aërial waves fall, that is, the point of the application of the pressure to the axis of rotation, is one and a-half times the distance

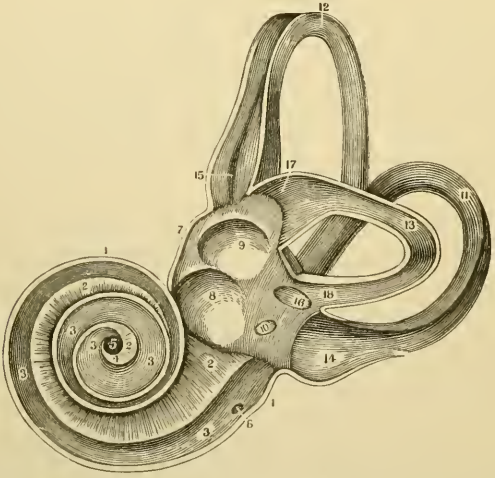
[1] Quelques Experiences d'acoustique, 1882, p. 29.

to the long process of the incus. Where the effect is produced the amount of movement of the stapes is only two-thirds that of the tip of the manubrium, the force exerted by the stapes is one and a-half times as great as that exerted by the tip of the manubrium. In other words, the parts involved are so disposed as to constitute a lever with unequal arms, the long arm carrying the light weight representing the distance from the manubrium to the axis of rotation, the short arm carrying the heavy weight the distance from the axis to the stapes. Such being the mechanical relation of the parts it follows that a motion of large amplitude but of little force, such as falls upon the tympanic membrane, becomes a motion of small amplitude but of great force, falling upon the fluid of the vestibule at the oval window. It is in this way that aërial waves, falling upon the tympanic membrane, are transformed into the water waves of the vestibule.

Structure of the Internal Ear.

The internal ear includes the labyrinth and the auditory nerve. The labyrinth, so-called on account of its highly complex structure, consists of the vestibule, semicircular canals, and cochlea. Though these parts are imbedded in the petrous portion of the temporal bone, their osseous walls are independent of the bony structure of the latter. This is well seen at birth, when the whole labyrinth can

FIG. 507.

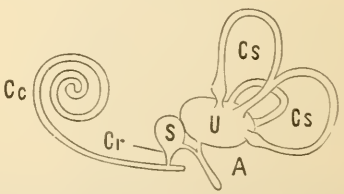


1, 2, 3. Turns of cochlea. 4. Fenestra rotunda. 5. Fenestra ovalis. 8, 9, 10. Posterior semicircular canal. 11. Superior semicircular canal. 12. External or horizontal semicircular canal.

be readily excavated from the surrounding loose osseous substance. The vestibule, situated between the tympanum and the internal auditory meatus, is a somewhat oval-shaped cavity about 5 millimeters ($\frac{1}{5}$ of an inch) in diameter, passing postero-externally into the semicircular canals, and antero-internally into the cochlea, and

communicating with the tympanum by the foramen ovale. The semicircular canals, so-called on account of their form, are three in number and are named from their position superior, posterior, and inferior, or external, the two former being disposed vertically, the latter horizontally. Each semicircular canal expands at one extremity into a bottle-like dilatation, the ampulla, which communicates with the vestibule. Of the undilated extremities two unite, and then with the remaining one also open into the vestibule. The three semicircular canals thus communicate with the vestibule by five orifices. The vestibule, semicircular canals, and cochlea, as well, are lined throughout with a thin periosteal membrane, which in passing over the foramen ovale and foramen rotundum thereby close these orifices. Within the cavity of this membrane is found a serous-like fluid, the liquor cotungii or perilymph of Breschet, an appropriate name on account of its surrounding the membranous labyrinth also containing a similar fluid, the endolymph of Breschet or liquor of Scarpa. The membranous labyrinth, so called on account of its membranous structure, and receiving the terminal filaments of the internal auditory nerve, floats in the perilymph within the bony labyrinth, with the walls of which it is more or less connected by delicate fibrous bands. The membranous labyrinth, like the osseous, consists of three parts, vestibule, semicircular canals, and cochlea. The membranous vestibule (Fig. 508), however, is composed of two distinct sacs or pouches, the utriculus (U) and sacculus (S), the former of which, the larger, occupies the hemi-elliptical fossa of the bony vestibule, and gives off three membranous semicircular canals, the latter, the smaller, occupies the hemispherical fossa and gives off through a narrow duct, the membranous cochlea.

Fig. 508.



Membranous labyrinth. Cs. Semicircular canals. U. Utriculus. S. Sacculus. A. Aqueduct of vestibule. Cr. Ductus reuniens. Co. Cochlea.

The sacculus and utriculus, while not communicating directly, do so indirectly through the membranous aqueduct (A) of the vestibule, the latter being formed through union of the small ducts proceeding from the sacculus and utriculus, respectively. Adhering to the inner surface of both the utriculus and sacculus, may be seen white, discoidal masses, consisting of minute crystalline particles of calcium carbonate, the so-called otoliths or otocoma. The membranous, semicircular canals, about one-third of the diameter of the osseous ones, in the perilymph of which they float, resemble the latter in form and general disposition, being three in number, disposed superiorly, vertically, and horizontally, expanding into ampullæ, and communicating with the membranous vestibule by five orifices. The membranous vestibule and semicircular canals,

consisting of three layers, an outer fibrous, an inner epithelial, and an intermediate membrana propria, receive, as already mentioned, the terminal filaments of the vestibular branch of the internal auditory nerve. The latter divides at the bottom of the internal auditory meatus into three branches, the first of which, passing through the pyramidal eminence of the bony vestibule at the superior cribriform spot, is distributed to the utriculus and ampullæ of the superior and inferior or horizontal semicircular canals; the second, passing through the hemispherical fossa at the middle cribriform spot, is distributed to the sacculus; and the third through the ampulla of the bony posterior semicircular canal at the inferior cribriform spot, to the ampulla of the membranous posterior semicircular canal. Just in those situations where the nerve fibers penetrate the membranous vestibule (macula acustica) and the membranous semicircular canals (crista acustica), their outer or fibrous layer is intimately associated through connective tissue with the bony wall of the vestibule and canals, the perilymph being here absent.[1] The ultimate nerve fibers having passed through the membranous vestibule and canals, finally terminate in what may be called the auditory epithelium, which appears to consist essentially of columnar cells intermixed with spindle-shaped ones supporting long, firm bristles, the auditory hairs (Fig. 509), which penetrate into the endolymph and support the otoliths. The otoliths, otocrania, or ear stones, are small, rhombic or octohedral crystals consisting of calcium carbonate with traces of other salts and organic matter. The function of the otoliths is very obscure. By some they are regarded as adjuvants, by others as dampers of sound waves. They have also been supposed to aid in some way the appreciation of the direction and extent of our movements.

FIG. 509.

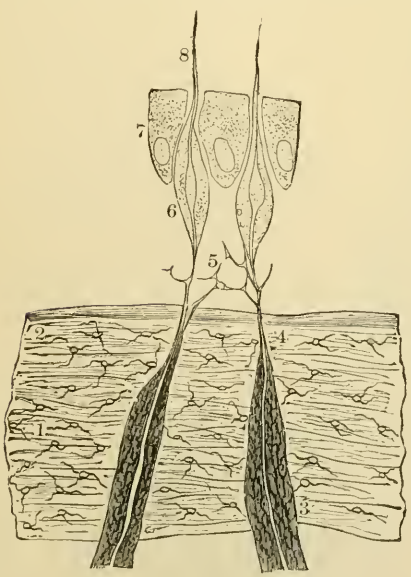


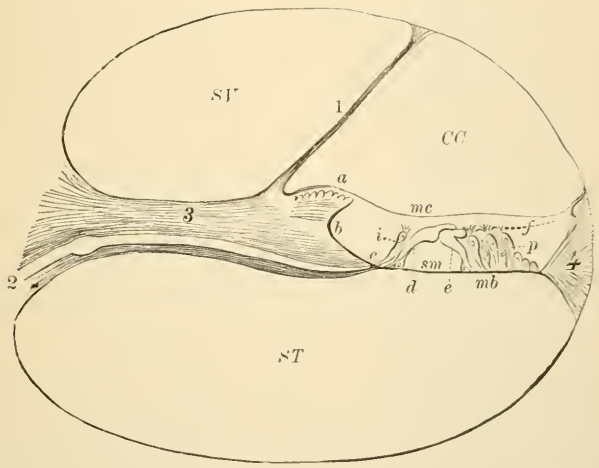
Diagram of the auditory epithelium, and the mode of termination of the nerves of the ampullæ. 6. Spindle-shaped cells, each supporting an auditory hair (8). 7. Basal supporting cells. 3, 4. Nerve fiber passing through the tunica propria to join the plexus in the epithelium. (M. SCHULTZE.)

Up to the present moment, in order to prevent confusion, we have purposely avoided mentioning, except incidentally, the bony

[1] M. v. Lenhossek, Beiträge zur Histologie des Nervensystems und der Sinnesorgane, 1894, s. 1.

or membranous cochlea, and yet it will be found that the cochlea, though, at first sight, resembling but little a semicircular canal, consists, like the latter, of a bony tube enclosing and attached to a membranous one, the latter floating in perilymph and containing endolymph. For simplicity sake, let us, in considering the structure of the cochlea, begin by disabusing our minds of it being a coiled tube, and regard it as a straight one, as it is throughout its whole length in birds, and at its commencement in man; and further, let us begin our description of its structure by supposing that we are viewing the cochlea at its commencement in transverse section, and endwise, as represented in Fig. 510. Looking at the cochlea

FIG. 510.

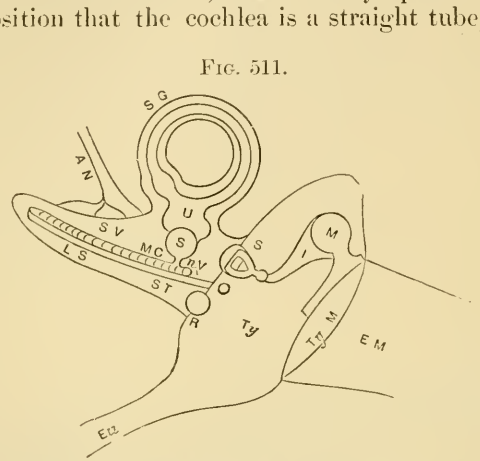


Section through one of the coils of the cochlea, diagrammatic. Mag. 30. *ST.* Scala tympani. *SV.* Scala vestibuli. *CC.* Canalis cochleæ. 1. Membrane of Reissner forming its vestibular wall. *a.* Limbus laminæ spiralis. *b.* Sulcus spiralis. 2. Cochlear nerve. 3. Lamina spiralis. *mc.* Membrana tectoria. *mb.* Membrana basilaris. *de.* Rods of Corti. 4. Ligamentum spirale.

from such a point of view, it will be seen to consist of a bony tube, divided by a septum partly bony (lamina ossea), partly membranous, into an outer and inner space, the latter communicating through the foramen rotundum with the tympanum, and called, therefore, the scala tympani; the former continuous with the bony cavity of the vestibule, and communicating, therefore, indirectly through the foramen ovale with the tympanum, and called the scala vestibuli. This may be at once shown by readjusting the cochlear portion of the section that we have just been considering to the remaining portion of the bony labyrinth, and passing bristles through the foramen rotundum and ovale, supposing the membrane passing across this opening and the stapes be removed. Conceiving, however, that the cochlea be a straight tube, and supposing it to be divided longitudinally, it will be found that the bony, membranous partition (Fig. 511) is absent at the end of the cochlea (helicotrema), the end

opposite to the vestibule, the consequence of which is that the bristles just passed through the foramen ovale from the tympanum, if continued onward, after traversing the scala vestibuli, will pass at the end of the cochlea into the scala tympani, and thence, through the foramen rotundum, reach the tympanum. Such being the relations of the scala vestibuli and scala tympani to each other and to the vestibule on the one hand, and to the tympanum on the other, on the supposition that the cochlea is a straight tube, it is obvious

FIG. 511.



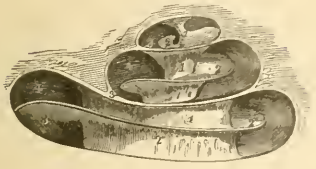
Diagrammatic view of the relative position of the parts of the ear. EM. External meatus. TyM. Tympanic membrane. Ty. Tympanum. M. Malleus. I. Incus. S. Stapes. R. Round window. O. Oval window. SG. Semicircular canal. U. Utriculus. S. Sacculus. V. Vestibule. SV. Scala vestibula. ST. Scala tympani. MC. Membranous cochlea. LS. Lamina ossea. Eu. Eustachian tube. AN. Auditory nerve.

that if the latter be turned two and a-half times upon itself around an axis or modiolus from right to left in the right ear, and the reverse in the left, the apex being situated downward, forward, and outward, that the above relations will not in any way be essentially changed. From an inspection of Fig. 510, representing the cochlea in transverse section, it will be observed, however, that the membranous portion of the septum dividing the interior of the cochlea into the scala vestibuli and scala tympani, and attached to the osseous wall by the ligamentum spirali, consists of two layers, a basilar membrane, and a tectorial membrane, a space intervening between the two, and that just at the point where the tectorial membrane is attached to the osseous lamina, which in the coiled tube is, of course, spirally disposed, a third membrane, the membrane of Reissner, passes obliquely across to the outer osseous wall.

As a matter of fact, however, as both ends of the cochlea are covered in by membrane, the vestibular scala is separated from the tympanic scala by a membranous tube which is given off by the membranous sacculus (Figs. 508, 511) through the ductus reuniens just as the membranous semicircular canals are given off by the utriculus, the other end of the membranous cochlear tube being attached by its pointed blind extremity to the wall of the cupola, the latter partly bounding the helico-

trema. And just as the membranous semicircular canal, filled with endolymph and floating in perilymph, is attached to the

Fig. 512.

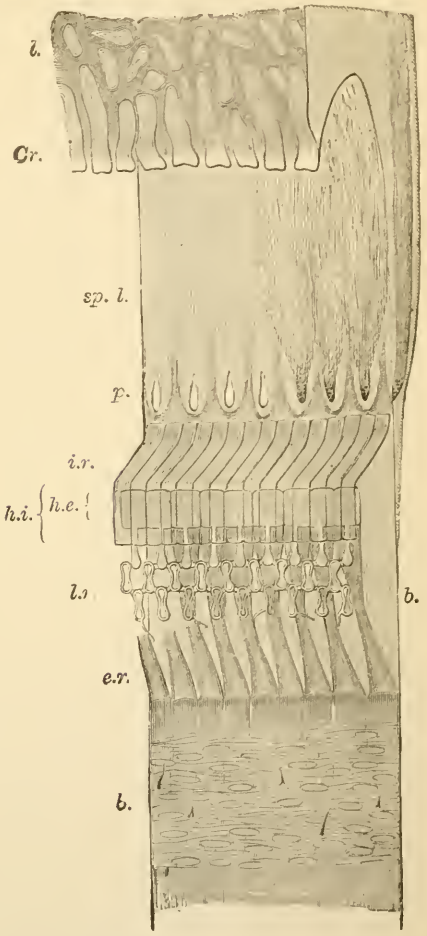


Diagrammatic view of the osseous cochlea laid open. 1. Modiolus or central pillar. 2. Placed on three turns of the lamina spiralis. 3. Scala tympani. 4. Scala vestibuli.

wall of the bony semicircular canal, so is the membranous cochlea, filled with endolymph and floating in perilymph, attached to the wall of the bony cochlea, the membranous cochlea, however, being spirally disposed like the bony cochlea enclosing it (Fig. 512). The membranous cochlea differs, however, from the membranous semicircular canal, not only in being coiled upon itself, but in the highly complex character of the structures lying in the space intervening between the basilar and tectorial membranes, known as the rods of Corti, which receive the terminal filaments of the cochlear branch of the internal auditory nerve.

The rods of Corti are stiff, rod-like bodies, disposed in two sets, an inner set and an outer set; the inner numbering about 6,000, the outer about 4,500. The inner rods being inclined outwardly, and the outer rods inwardly, the two sets of rods meet at their heads, the space between the rods—that is, between the latter and the basilar membrane—being known as the canal of Corti. The inner

Fig. 513.



Semi-diagrammatic view of part of the basilar membrane and tunnel of Corti of the rabbit, from above and the side. Much magnified. *l.* Limbus. *Cr.* Extremity or crest of limbus with teeth-like projections. *bb.* Basilar membrane. *p.* Perforations for transmission of nerve fibers *N*, which are represented at the lower part of the figure, but omitted for the sake of clearness in the upper. *ir.* Fifteen of the inner rods of Corti. *hi.* Their flattened heads seen from above. *er.* Nine outer rods of Corti. *he.* Their heads, with the phalangeal processes extending outward from them and forming, with the two rows of phalanges, the lamina reticularis. *tr.* The fibers of the outer rods are seen to be continued into the striation of the basilar membrane, through which the connective tissue fibers and nuclei of the undermost layer are seen. Portions of a few of the basilar processes of the outer hair-cells remain attached to the membrane. (QUAIN and SHARPEY.)

rods support on their inner surface one row of epithelial cells, the inner hair cells, so called on account of their terminating in short, stiff hairs; the outer rods on their outer surface three or four rows of similar cells, though somewhat more elongated than the outer hair cells. The hairs of the latter pass through ring-like structures, the reticulum, attached to the heads of the outer rods. Both the outer and inner hair cells, in all probability, receive, directly or indirectly, the terminal filaments of the cochlear nerve (Fig. 513). The latter, after passing through the foramina of the spiral tract at the bottom of the internal auditory meatus, ascend through the axis of the cochlea, and thence traversing the lamina ossea spiralis perforate the basilar membrane, and so reach, by intermediate filaments, the hair cells. Bearing in mind that the base of the stapes is adherent to the periosteum lining the vestibule and covering the foramen ovale; it is evident that the vibrations of the tympanic membrane, in being transmitted through the ear bones to the perilymph filling the bony labyrinth, will throw into vibration the endolymph filling the membranous labyrinth and the hairs projecting into it, and consequently the auditory nerve, regarding, as we do, the hairs as the terminal filaments of the vestibular and cochlear nerves, into which the auditory nerve divides in the meatus, whence the vibrations, in being further transmitted, more especially by the fibers of the cochlear nerve, to the temporo-sphenoidal convolutions of the cerebrum, give rise to the sensation and perception of the sound. With reference to the function of the membrane covering the foramen rotundum, the membrana secondaria, which consists on the tympanic side of the mucous membrane, and on the cochlear, of the periosteal layer lining the scala tympani of the cochlea; while nothing is positively known, in all probability it is pushed outward, as the stapes is pushed inward, which would obviously be of advantage in absorbing some, at least, of the superfluous sonorous wave motion. Such being, in general, the disposition and relation of the parts of which the internal ear is composed, and the manner in which the auditory nerve is distributed to it, is thrown into vibration, it is to be expected that such a complexity of structure is correlated with a corresponding differentiation in function. As a matter of fact, however, little has been definitely established as regards the specific functions of the vestibule, semicircular canals, and cochlea, which is due, no doubt, to any experimental investigation being so difficult on account of the nature of the case, and from the pathological and clinical data on the subject being so meagre and unreliable in character. In the absence of such evidence the facts of comparative anatomy have been appealed to as a means of elucidating the functions of the internal ear. It is well known to anatomists that the organ of hearing exists in the lower animals in a very rudimentary condition; thus, in certain of the crustacea, for example, the ear consists of an invagination of the tkin, a cutaneous pit lined with hairs, situated in the basal joint of she internal antennæ, which may remain open and contain particles

of sand, or may be closed and enclose calcareous otoliths. A similar vesicle, lined with ciliated epithelium, and containing otoliths, is also found in the mollusca situated upon the infra-œsophageal portion of the nervous collar surrounding the alimentary canal. On the supposition that the vesicle just described as occurring in the crustacea and mollusca, and even in lower forms of life, as in the annelida, hydrozoa, etc., is a rudimentary organ of hearing, its functions must be limited almost entirely to the appreciation of the intensity or loudness of sounds—at least it is difficult to conceive of animals, relatively so lowly organized, being affected to any very great extent by difference in pitch and quality. If such is the case, and it be admitted that this vesicle, or otocyst of the lower animals, is the homologue of the vestibule of the higher, which the study of the development leads us to suppose, then it follows that the function of the vestibule in man is the appreciation of the intensity of sound. In passing from the invertebrata to the vertebrata, and more particularly to the fishes, we find, with the exception of the amphioxus, in which the ear is absent altogether, that the organ of hearing becomes more complex as we ascend through the successive forms of piscine life. Thus, in the myxine, the ear consists of a vestibule with one semicircular canal; in the lamprey of a vestibule with two semicircular canals; and in the teleosts of three with a rudimentary cochlea as well. Now, while it is evident that it would be of advantage to fishes to be able, not only to distinguish loud from low sounds, but also the direction from which the sounds proceed, the appreciation of melodious and harmonious ones would be of but little use, and since the homology of the semicircular canals of the lower vertebrates with those of the higher ones is undoubted it is still held by some physiologists that our appreciation of the direction of sounds is connected in some way with these structures. However that may be, experiments upon animals and clinical and pathological observation in man already referred to have shown conclusively that the maintenance of equilibrium depends, to a certain extent, at least, upon the integrity of the semicircular canal.

To what extent the inability in maintaining equilibrium in such cases is due to the hearing being impaired, and how much to the transmission of the afferent impressions to the cerebellum being interfered with, upon which the maintenance of equilibrium partly depends, is difficult, if not impossible, to determine exactly. By a method of exclusion, then, the inference is rather forced upon us, that our sensation of tone depends, in some way, upon the cochlea, the structure of which undoubtedly suggests that its function is rather concerned with the appreciation of the quality of sound, a sort of universal resonator, than with that of pitch or intensity. Regarding the rods of Corti, and the hair cells lying upon them, as so many piano keys and strings appropriately tuned, it is obvious that it would analyze sounds, like a series of resonators.

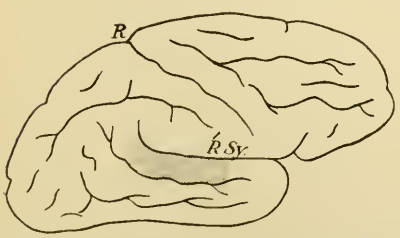
The objection offered to the above ingenious view of Helmholtz, that the rods of Corti being absent in the rudimentary cochlea of birds,

cannot be essential for the recognition of tones, is not a necessarily fatal one, since, though many birds can sing, it does not follow that their sensations and ideas of melody and harmony should be as developed as that of man; on the contrary, in the absence of a complex brain, it is difficult to comprehend how they should have any considerable appreciation of musical sound.

A more important objection than that just mentioned is that the length and disposition of the rods of Corti do not vary to the extent that the hypothesis of Helmholtz demands. It has been suggested, therefore, that it is the basilar membrane present in birds as well as mammals that vibrates sympathetically rather than the rods of Corti, the basilar membrane being regarded as consisting of parallel strings of different lengths, tensed radially, but relaxed longitudinally, conditions which are consistent with the mechanical theory involved.

It would appear, therefore, that the so-called auditory nerve consists really of two different nerves, the cochlear nerve, the auditory nerve proper, the pathway for the impulses giving rise to hearing, and the vestibular nerve transmitting the impulses upon which the maintenance of equilibrium depends and possibly those by which we appreciate the direction of sounds. In accordance with this view the cochlear and vestibular nerves, as might be expected, pass by different routes from the periphery to the cortex. The fibers of the cochlear nerve appear to arise from cells in the spiral ganglion and from the anterior auditory nucleus of the cerebellum, and pass thence by the tubercle acusticum and by the striæ medullares, into the lemniscus of the opposite side, and so to the posterior quadrigeminal and internal geniculate bodies of that side into the internal capsule[1] to terminate in the first and second temporal convolutions of the cortex (Fig. 514). The vestibular nerve lying ventrally to the cochlear nerve passes between the restiform body and the descending root of the fifth nerve to terminate in three distinct nuclei situated in the floor of the fourth ventricle and known, respectively, as the chief nucleus, the nucleus of Deiters, and the nucleus of Bechterew. In all probability the fibers of the vestibular nerve terminate in a distinct cortical center, situated in the temporal lobe in the neighborhood of that of the cochlear nerve.[1]

Fig. 514.



Position of the auditory center in the first temporal convolution. (Gowers.)

In conclusion, it must not be forgotten that whatever function be assigned to the different parts of the internal ear, that the cause of the sensation of sound, like that of color, is psychical, and, in its subjective aspect, is as little understood in the one case as the other.

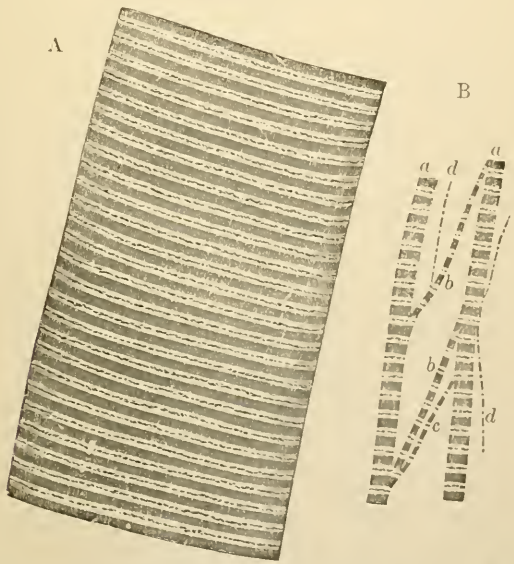
[1] Edinger, op. cit., s. 360. Rauber, op. cit., Band ii., s. 830. Obersteiner, op. cit., s. 412.

CHAPTER XLIV.

IRRITABILITY, CONDUCTIVITY, AND CONTRACTILITY OF MUSCLE.

In considering the subject of nervous irritability, it will be remembered that the contraction of a muscle following stimulation of the nerve supplying it, was taken as an indication and measure of the changes occurring in the latter. The changes undergone by the muscle itself, however, during its contraction remain still to be described. Muscles are of two kinds, striped and unstriped, of which the former will be first studied. Striped muscles, such as the skeletal muscles, heart, diaphragm, etc., consist of fasciculi or bundles of fibers separated by connective tissue, the latter being prolonged from the outer envelope or perimysium covering the muscle. Each muscular fiber is a more or less cylindrical tube from 3 to 4 cm. (1.2 to 1.6 of an inch) in length, and between $\frac{1}{4}$ and $\frac{1}{24}$ of a mm. ($\frac{1}{100}$ and $\frac{1}{600}$ of an inch) in diameter, and con-

FIG. 515.



A. Portion of a medium-sized human muscular fiber (magnified nearly 800 diameters). B. Separated bundles of fibrils, equally magnified. *a, a.* Larger, and *b, b,* smaller collections. *c.* Still smaller. *d, d.* The smallest which could be detached. (KIRKES.)

sists of three parts, the sarcolemma or sheath, the sarcous substance, and the nuclei or muscle corpuscles. The sarcolemma is the elastic,

transparent, structureless, and colorless sheath enclosing the sarcous substance. The latter, being marked transversely by alternating light and dark bands, is said to be transversely striate. If fresh muscular fiber be examined in its own juice, not only the light and dark bands just referred to will be seen, but it will be observed (Fig. 515) that the light band is divided into two by what looks like a line, the so-called line of Krause, Dobie or sarcoplasm, the portion of the fiber intervening between the latter, constituting the sarcous substance or sarco-styles. The sarcous substance appears to consist of a broad, dim, doubly refracting or anisotropous contractile disk, both ends of which are capped by a layer of clear, homogeneous, single refracting (isotropous), soft or fluid substance. The nuclei or muscle corpuscles lie immediately under the sarcolemma, their long axis being in the long axis of the fiber, and in all probability generate the sarcous substance. As already mentioned, muscles being active organs are well supplied with blood, and with sensory as well as motor nerves; the sensibility of muscles is relatively, however, but slight. The second variety of muscle, the non-striped or smooth, occurring among other situations in the alimentary canal, arteries, ureter, etc., consists of fusiform or spindle-shaped cells with tapering ends, varying in length from $\frac{1}{25}$ to $\frac{1}{50}$ of a millimeter ($\frac{1}{600}$ to $\frac{1}{1200}$ inch) and in breadth from $\frac{1}{250}$ to $\frac{1}{100}$ of a millimeter ($\frac{1}{6000}$ to $\frac{1}{25000}$ inch). Within each cell may be seen after the addition of acetic acid, a solid, oval, elongated nucleus, containing one or more nucleoli, in which the motor nerves derived from the sympathetic and consisting of both medullated and non-medullated fibers, appear to terminate. Non-striped muscle, while freely supplied with blood, is not, however, so vascular as the striped variety. Striped muscle or ordinary flesh is either neutral or slightly alkaline in reaction, and consists chemically by weight, of three-fourths water and one-fourth nitrogenous, non-nitrogenous matters, and salts. Of the nitrogenous matters the most important is the coagulable substance that becomes in dead rigid muscle myosin, though albuminates, creatin, xanthin, hypoxanthin, taurin, inosic and uric acids are also present. Among the non-nitrogenous matters may be mentioned paralactic (sarcolactic) acid, muscle sugar, glycogen, dextrine, and glucose. Of the salts, the principal ones are the alkaline phosphates, potassium and sodium chloride. But little is known of the chemical composition of unstriated muscular tissue beyond the fact of it consisting of water, nitrogenous and non-nitrogenous bodies.

Let us turn now to the consideration of some of the more important properties of muscle, many of which, such as irritability, conductivity, and contractility, have already been incidentally referred to in the consideration of the nervous system. The irritability of muscle, like that of nerve, is excited by sudden blows, pinching, cuts, etc.; by sudden and extreme changes in temperature, and is altered by solutions of all kinds, except those resembling in their

composition serum and lymph. The irritability of muscle is also influenced like that of nerve by the strength, density, rate of change in intensity, duration, and angle of application, of the electrical current.

It will be remembered, that by attaching a lever to a muscle and connecting the pen of the same with the recording cylinder or the plate of the pendulum myograph, that we obtained a trace, the muscle curve, and that by means of suitable chronographic apparatus we determine the latent period, the moment of the beginning, maximum, and end of the muscular contraction.

It may be also mentioned in this connection that the excitement developed through the stimulation of a muscle with a galvanic current begins with a closing current at the kathode and spreads thence through the muscle, whereas that developed with an opening one begins at the anode, and that such is the case, whether the current is a descending or an ascending one. As in the case of the injured nerve, so also in that of the injured muscle, it can be shown by means of the galvanometer that a difference of electrical potential exists between the longitudinal uninjured surface and the transverse cut, one giving rise to a "current of rest," the direction of which is from the longitudinal to the transverse surface. The electro-motive force of the current of rest of muscle, as determined by the round compensator, amounts to the 0.069 of a Daniel element. The resistance offered by muscle to the transmission of an electrical current in a longitudinal direction, as compared with mercury, is in the ratio of 2,006,000 to 1, and in a transverse one in the ratio of 13,103,000 to 1.[1] The "current of rest" of muscle, like that of nerve, undergoes also during its activity a "negative variation," exhibits a current of action which travels[2] at the rate of 3 meters (9.8 feet) per second, with a wave-length of 10 mm. ($\frac{1}{5}$ of an inch), accompanied by a visible contraction wave, which travels at about the same rate, but with a wave-length of from 200 to 400 mm. (8 to 16 inches), and shorter. If a portion of living irritable muscle of an insect, that of Telephorus, for example, be viewed under the microscope, the contraction waves observed passing along the fibers may be fixed by appropriate treatment with osmic acid, and so compared with the remaining portion of the fiber at rest. By such method of investigation, it has been shown, that while the dark and light bands so characteristic of striated muscle at rest are still observable in the muscle when contracted, the relation of the two is reversed, that is to say, the dark band in the contracted muscle corresponds to the light band in the quiet one, and *vice versâ*, the distinction between light and dark bands not being observable, however, during the intermediate stage between rest and contraction. While there is still some difference of opinion as to

[1] H. C. Chapman & A. P. Brubaker, Researches upon the General Physiology of Nerve and Muscle, Proc. Acad. of Nat. Science, Phila., 1888, pp. 106, 155.

[2] Bernstein, Untersuchungen, s. 58. Heidelberg, 1871.

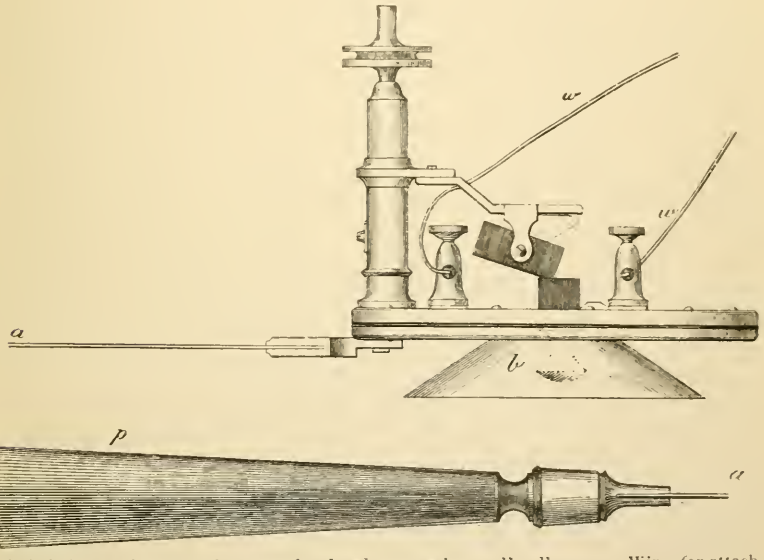
the interpretation of all of the appearances of such a preparation, the same makes very evident the swelling and shortening of the fibers, which is brought out even better if the object be viewed by polarized light.

In describing the induction apparatus of Du Bois Reymond, it will be remembered that the secondary coil can be removed as desired from the primary and the strength of the stimulus thrown into the nerve or muscle in this way varied. Beginning with a very weak stimulus and gradually increasing the same, the corresponding contraction will be found to increase, at first rapidly, then more slowly, until a maximum is reached, then to diminish until contraction finally ceases through the muscle being fatigued from repeated stimulation. If the distance through which the secondary coil be slid along be laid down as the abscissa line and the extent of contraction as the ordinates, the curve obtained will be the graphic representation of the contraction considered as a function of the stimulus. It should be mentioned, in this connection, that while muscles in the body, where they are on the stretch after contraction, return at once to their initial length, out of the body they fail to do so either as completely or as quickly, the rapidity and extent of the return appearing to depend upon the nutrition of the muscle. Suppose that instead of varying the electrical stimulus, as in the case just mentioned, we maintain it as constant as possible, but that we place in the little scale pan suspended from the lever attached to the muscle successively 10, 20, 30, 40, and 50 grammes—that is, we gradually increase the weight the muscle has to lift to increase the resistance that it has to overcome. Contrary to what might naturally be expected, the resistance offered to the contraction, for a time at least, increases the contraction, then with a continued increase of weight, the contraction having reached a maximum, gradually diminishes until finally it ceases altogether. If the weights be regarded as the abscissas and the extent of contraction as the ordinates, then the curve obtained will represent the contraction regarded as a function of the resistance. It will be observed, in experimenting with weights, that a stretched muscle reaches quickly its initial length after the extending cause has been removed, the elasticity not being very great but perfect. Contrary, however, to what might have been expected, the extensibility is not diminished during contraction but increased, so that the muscle has to overcome the resistance due to its extensibility before it can raise any weight. Thus, suppose that a muscle be extended a given extent by a weight of say 40 grammes during rest, and then that it be unloaded and thrown into a state of tetanus and then again loaded with the same weight, the extension in the latter case will be greater than in the former. It will also be learned, by experimenting with gradually increasing weights, that finally the elongation of the muscle due to its elasticity is exactly compensated by the shortening due to its contraction, such a contraction of static

equilibrium being reached in the case of the frog, the transverse section being one square centimeter and the weight 692 grammes, and in man the muscles being those of the calf of the leg, and the weight 8 kilogrammes (17.6 lbs.).

The work done by a muscle, like all work, is estimated by the height through which a weight is raised. Thus, if 5 grammes (77.1 grains) are raised 27 millimeters (1.08 inch) by the muscle of a frog, then 27×5, or 135 grammes millimeters (83 grain inch) work is done by such a muscle. By gradually increasing the weights and noting the heights through which they are raised, it will be found that the work done gradually increases as the weight increases until a maximum is reached, after which there is a gradual diminution until the muscle, as in the former instances, ceases to contract. The fatigue experienced by muscle during prolonged

FIG. 516.



Helmholtz's myophone. *b*. Button to be placed on muscle. *a*. Handle. *w*, *w*. Wires for attachment to telephone.

contraction, which sooner or later brings the latter to an end, appears to be due to the accumulation of the waste effete products incidental to its activity. Within certain limits such matters are eliminated as rapidly as formed and new materials for the repair of the muscle are at the same time supplied. If, however, the contractions follow each other very rapidly, sufficient time is not allowed for the accomplishing of these processes, and the equilibrium between disassimilation and assimilation is no longer maintained. While the cohesion and irritability of muscle are diminished by fatigue, the elasticity is but little, if at all, affected. The latent period is, however, lengthened. During fatigue the extent of con-

traction is smaller and the latter lasts longer than when the muscle is fresh, the return to the initial length is also slower. As might be expected, a muscle is fatigued much sooner when it does work than than when it simply contracts without doing work. If a stethoscope or myophone (Fig. 516) be applied over a powerfully contracting muscle, the biceps, for example, a deep, low tone will be heard, the pitch of which is about 40 vibrations a second, and which is, without doubt, due to the successive shortenings which make up a muscular contraction, the latter caused, in all probability, by 40 nervous impulses being transmitted to the nerve centers along the motor nerves to the muscle. We say that the pitch of this muscular sound or tone is 40 vibrations per second and caused by 40 nervous impulses, because that is the note actually heard, and because we can produce such a note experimentally out of the body by stimulating the nerve that number of times.

It should be mentioned, however, that according to most physiologists, the muscular sound heard when the biceps contracts, while due to 40 vibrations per second is really the first overtone or first octave above the fundamental, the latter being due to 20 vibrations per second. If such be the case, then the muscle contracts only 20 times a second, the pitch of the muscular sound produced is 20 vibrations a second, and the nerve is stimulated 20 times a second. Whether the muscular sound heard be the fundamental note or the octave above, in either case, however, the mechanism of its production is the same—that is, due to muscular vibration. It will be remembered that in accounting for the first sound of the heart, muscular contraction was assigned as one of the causes, and while there is no doubt that it is an element in the production of the first sound, it must be admitted that it is difficult to understand how the contraction of the heart, if a simple one, can give rise to a muscular sound, which we have just seen is produced by numerous contractions. Facts of this kind, as well as peculiarities in the muscular structure of the heart itself, lead one to suppose that possibly the contraction of the heart during its ventricular systole is rather of a tetanic than simple character, as is usually supposed. The muscle sound or muscle tone due to successive muscular contractions must not be confounded with what is unfortunately called muscular tonus or muscular tonicity, by which is meant the state of tension due to the muscles in the living body being more or less stretched between their attachments. Such being the case, when a muscle is divided transversely it contracts, the two parts receding from each other. The sphincter muscles, however, do not appear to be stretched during repose, but only when they are dilated. On the other hand, by the term muscular tone, as understood more especially by neurologists, is meant the firmness or tone of muscle due to continued nervous excitement emanating from the spinal cord. By some physiologists, however, it is denied that the spinal cord exerts any such tonic influence upon the muscles, and yet it is well

known that a decapitated frog will remain in a sitting posture as long as the spinal cord is intact, but that with its removal the limbs fall apart. Further, the limbs of a decapitated turtle, and, to a certain extent, those of a decapitated rabbit, also retain their firmness, tone, but with the removal of the spinal cord become lax, flaccid. Such facts are incomprehensible unless it be supposed that the muscles are maintained firm, elastic, resilient through the influence of the spinal cord. As the influence exerted by heat, blood supply, etc., upon the activity of the muscle is essentially the same in the case of muscle as in that of nerve, it will not be necessary to dwell further upon the same in this connection. If living contractile frog's muscle, freed as much as possible from blood, be frozen and then minced and rubbed up in a mortar with four times its weight of snow containing 1 per cent. of sodium chloride, a mixture will be obtained, which at about 0° Cent., can be filtered. The filtrate so obtained, or muscle plasma, at first fluid, becomes, at ordinary temperature, jelly-like, and then separates into a clot and serum, the action, which before coagulation was neutral, or slightly alkaline, now being distinctly acid. The serum contains albumin and extractives; the clot consists of myosin, a substance intermediate in character between fibrin and globulin. It will be observed as in the case of the fibrin of the blood, that myosin does not exist as such in living contractile muscle, but that it is developed during the coagulation of the same out of some preëxisting albuminous element or elements. The myosin so developed from living muscle does not differ at all from the myosin obtained by appropriate chemical manipulation from dead muscle. Indeed, the passage of a muscle into the condition of rigor mortis, characterized by loss of its irritability, softness, translucency, extensibility, and elasticity may be regarded as being essentially due to the coagulation of its muscle plasma, to the development of myosin out of its preëxisting albuminous elements. Since living muscle during its contraction becomes distinctly acid from having been previously faintly alkaline or neutral, from a considerable amount of lactic and sarcolactic acid being set free, as in the condition of rigor mortis, from the fact of the muscle, as in the latter distinction, becoming rigid, it might, at first thought, be supposed that the changes occurring during the contraction of the living muscle are essentially the same as those occurring in rigor mortis, due to the oxidation of some complex albuminous material elaborated and stored up in the muscle during its periods of repose. That the phenomenon of muscular contraction is not, however, identical with that of rigor mortis, is shown by the important fact that during muscular contraction no myosin is developed, upon the formation of which the phenomenon of rigor mortis depends, and that during contraction the extensibility of the muscle is increased, instead of being diminished, and that it does not lose its translucency.

But little is positively known as to the physical and chemical

changes undergone by unstriated muscular fiber during death or contraction; from what has been established, however, we are led to believe that the processes going on in unstriated muscle fiber differ in degree rather than in kind from those just described as occurring in striated muscle. While the limits of this work do not permit of any discussion of general muscular movements which would involve a detailed description of the muscles and joints and the consideration of animal mechanics, a brief account of how ordinary movements are performed does not appear inappropriate in concluding this chapter. The greater part of the skeletal muscles may be regarded as so many sources of power for moving the bones viewed as levers. The levers are of three kinds or orders according to the relative position of the power, the weight to be moved, and the axis of motion or fulcrum. In a lever of the first kind, as in Fig. 517, A, the power (P) is at one end, the weight (W) at the other, and the fulcrum (F) in the middle. As a familiar ex-

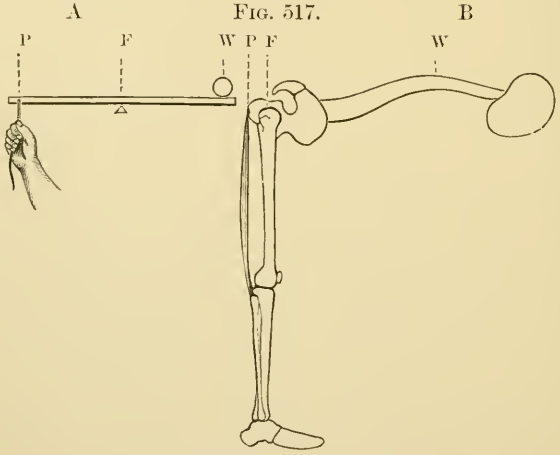


FIG. 517.

Illustration of lever of first order. (KIRKES.)

ample of the first kind of lever, occurring in the human body, may may be mentioned the raising of the body from the stooping posture by the action of the hamstring muscles attached to the tuberosity of the ischium (Fig. 517, B). In a lever of the second kind (Fig. 518, A), the power is at one end, the fulcrum at the other, and the weight in the middle. The depression of the lower jaw in the opening of the mouth is an illustration of a lever of the second kind (Fig. 518, B), in which the tension of the muscles elevating the jaw represents the weight. In a lever of the third kind (Fig. 519, A), while the fulcrum and weight are at either end, the power is in the middle. The flexing of the forearm by the action of the biceps muscle (Fig. 519, B) is an instance of this form of lever in the body. The different movements of the foot offer an illustration of

all three kinds of levers: of the first kind when the foot is raised and the toe tapped upon the ground, the ankle joint being the ful-

FIG. 518.

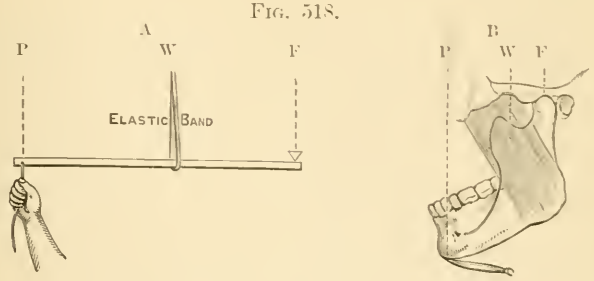


Illustration of lever of second order. (KIRKES.)

crum (Fig. 520, I); of the second when the body is raised upon the toes, the ground being the fulcrum (Fig. 520, II); of the third

FIG. 519.

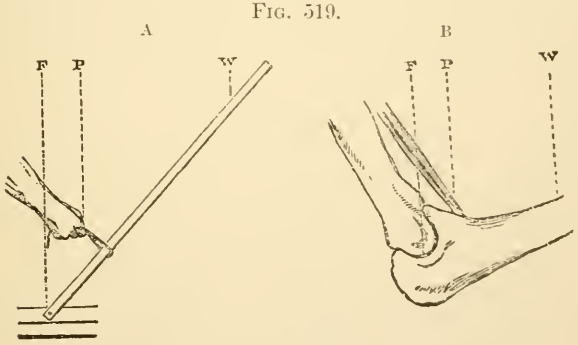


Illustration of lever of third order. (KIRKES.)

kind, when one dances a weight up and down by moving only the foot, the fulcrum being the ankle-joint (Fig. 520, III). As a gen-

FIG. 520.

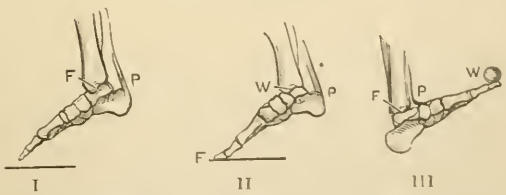
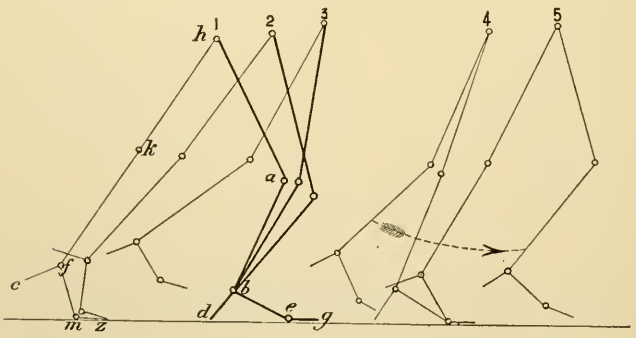


Illustration of levers of all three orders.
W. Weight of resistance. F. Fulcrum. P. Power. (HUXLEY.)

eral rule, in the human body, the power is so disposed with reference to the fulcrum, that while a greater range of motion is acquired

the power is diminished. Thus, in the case of the action of the biceps, it is evident that a great amount of force must be put forth to move the forearm, but that a considerable range of movement is obtained through a relatively slight shortening of the muscular fibers. In the act of standing, as accomplished by muscular action, the body is in a vertical position of equilibrium, a line drawn from the center of gravity of the body falling within the feet placed upon the ground. The head is firmly fixed upon the vertebral column by the cervical muscles pulling from the latter upon the occiput, and the vertebral column itself being fixed by the longissimus dorsi and quadratus lumborum muscles. In the sitting position the head and trunk, together constituting an immovable column, are supported upon the tubera ischii. In the forward posture the line of gravity passes in front, in the backward posture behind, and during the erect posture between, the tubera ischii. In walking, the two legs act alternately, the one leg, the active or supporting leg, carrying the trunk, the other leg being inactive or passive. The act of walking, for convenience of description, may be considered as made up of two acts. Act 1st (Fig. 521): the active leg being vertical and slightly flexed at the knee, alone supports the center of gravity of the body,

FIG. 521.



Phases of walking. The thick lines represent the active, the thin the passive, leg. *h*. The hip-joint. *k, a*. Knee. *f, b*. Ankle. *c, d*. Heel. *m, e*. Ball of the tarso-metatarsal joints. *z, g*. Point of great toe. (LANDOIS.)

the passive leg touching the ground with the tip of the great toe (2) only. At this moment the position of the leg corresponds to a right-angle triangle in which the active leg and ground represent the two sides, the passive leg the hypothenuse. Act 2d: the active leg being inclined, moves forward to an oblique position, the trunk moves forward, the active leg being at the same time lengthened that the trunk may remain at the same height. The latter is accomplished by extension of the knee (3, 4, 5) and the lifting of the heel from the ground (4, 5,), until the foot finally rests upon the ground by the point of the great toe. As the active leg is extended

and moves forward the tips of the toes of the passive leg leave the ground (3), and being slightly flexed at the knee-joint perform a pendulum-like movement (4, 5), the passive foot passing as far in front of the active leg as it was previously behind it. The foot being then placed flat upon the ground, the center of gravity is transferred to what now becomes the active leg, the latter being slightly flexed at the knee and placed vertically. The first act is then repeated, and so on. It will be observed that during walking the trunk leans toward the active leg and inclines somewhat forward, the effect of which is to overcome resistance of the air, and that it slightly rotates on the head of the active femur. Running differs from rapid walking in that at a particular moment, both legs not touching the ground, the body is raised in the air, the necessary impetus being given to the body by the forcible extension of the active leg.

CHAPTER XLV.

REPRODUCTION.

Spontaneous Generation. Fissiparous, Gemmiparous, and Sexual Generation.

At an immensely remote period the earth must have been entirely destitute of life, at least the physical conditions of the azoic period of geologists, and the æons preceding it were such as to make the existence of life, as we are acquainted with it, impossible. Whether the nebular hypothesis of the earth having been cast off from the sun be accepted or not, there can be no doubt that at an inconceivably distant period the earth was in a fluid or semi-fluid molten condition, and its temperature so high as to render life impossible, or even to admit of the union of the chemical elements composing it, the latter existing then separately, as they do in all probability now, in the sun, as shown by spectral analysis. The basalts, prophyries, and lavas entering into the formation of the igneous rocks, the volcanic action constantly going on at the present day in many parts of the world, the seismic disturbances, the high temperature of mines, etc., not only prove that originally the world was but little else than a ball of fire, but also that the fire, far from being extinguished, is only now restricted to the inner subterraneous regions lying under the crust of the earth. If speculation be admitted, we can conceive how with the loss of heat and the lowering of the temperature through the combination of hydrogen and oxygen the water was formed, and that gradually through the combination of the chemical elements the binary and ternary salts entering into the formation of the rocks constituting the crust of the earth were next produced, and finally, the physical conditions being suitable, that the combination of carbon, hydrogen, oxygen, nitrogen, and phosphorus or sulphur atoms, resulted in the development of protoplasm, or the simplest kind of life. While it is true that there is no evidence whatever that life now is ever generated otherwise than from preëxisting life, solitary tapeworms, maggots, etc., often cited by the uneducated as instances of animals spontaneously generated, offering no exception to the rule, being in reality reproduced, like all life, by preëxisting animal life, that the first life appearing upon the face of the earth was, nevertheless, spontaneously generated, developed independently of preëxisting life must be admitted, since there was no antecedent life during the azoic period to give rise to it. As to the inconceivability of how spontaneous generation was brought about, of how protoplasm, with its remarkable properties, was ever de-

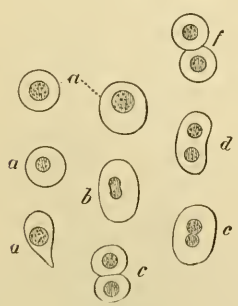
veloped through the combination of chemical elements possessing different properties, it may be said that it is just as difficult to comprehend how the combination of acid and base will give rise to a salt exhibiting properties possessed by neither, or how two gases like oxygen and hydrogen in combination produce a liquid, water, different from either. In either case we must suppose that the properties of the substance formed, however remarkable, are the sum of the properties of the elements entering into combination and giving rise to the substance, whatever is true of the inorganic in this respect being true of the organic as well, the question in either case being one of the redistribution of matter and energy only. Admitting that life originated spontaneously, there is little reason, however, to hope that the physical conditions which obtained when life first appeared upon the face of the earth can ever be realized experimentally so as to enable one to generate life *de novo*. Still it must not be forgotten that what appears impossible to one age becomes perfectly so to a succeeding one. Life having once appeared upon the face of the earth, however produced, there is no reason to suppose that it has ever been entirely absent, since catastrophies, such as volcanic eruptions, earthquakes, floods, climatic changes, etc., which are so destructive to life, are relatively local in action. Further, the first life, out of which all life has since been gradually developed, must have been of the simplest kind; indeed, so simple as to make it difficult, if not impossible, to say whether such life should be regarded as animal or vegetable, its characters being intermediate between, and partaking of the nature of both plants and animals. The latter, judging from their remains as presented in the Cambrian and Silurian rocks, or such as immediately overlie the azoic strata, were also at first of a simple kind. Thus among the plants and animals living in these early ages of the primary period of geologists may be mentioned seaweeds, jelly fish, coral-making polyps, crinoids, brachiopods, various kinds of mollusca, trilobites, etc. Passing on through the later ages of the primary period, the life becomes more varied and complex; fishes, ganoids, and sharks, and land plants, pine-like lepidodendrons, and ferns making their appearance during the Devonian age, or that of the sandstone, and reptiles in the carboniferous age, or that of the coal period, remarkable also for the richness of its cryptogamous plants. As the ages rolled on, during which the Jura rocks were deposited in Switzerland, the chalk cliffs in England, the marls in New Jersey, phanerogamous, or flowering plants, palms and trees like those of our own forests, oaks, dogwoods, poplars, beeches, appeared, while among the animals that lived during these ages may be mentioned fishes resembling those of the present day, gigantic reptiles, birds, and probably a few marsupial mammals.

During the tertiary period that followed, the flowering plants and trees then flourishing resembled closely those of the forests of the

present day, the invertebrate forms of life differed but little from those existing now, the fishes and reptiles were similar to those found in our rivers, oceans, and forests; while herbivorous animals, resembling the tapir, peccary, camel, deer, horse, rhinoceros, and elephant, roamed in herds over the continents, hippopotami wallowed in the streams; while beasts of prey were also numerous, being represented by animals closely allied to the lion, tiger, hyena, dog, and panther of the present day. During the close of the Tertiary, or, rather, of the post-Tertiary period, the general aspect of the world differing but little from that presented by it now, man appeared but in a condition of development probably far lower than that of the lowest existing savage, and the process of civilization began.

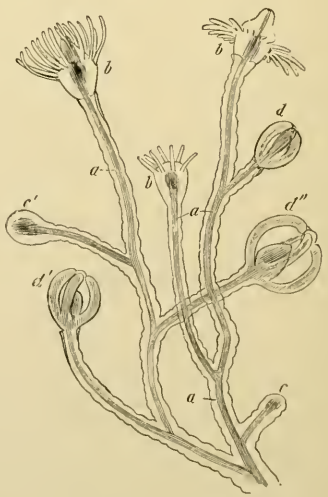
The idea of reproduction is usually associated with that of the difference of sex; the production of offspring naturally suggesting the idea of two parents. Many plants and animals, however, are reproduced entirely independently of sexual intercourse, by what is known as fission or gemmation; and as many of the structures of the body are developed by these processes, it is essential that they should be at least briefly illustrated. By the process of fission is meant the division of the single parent organism into two or more parts, each of which will become a new being, similar in form, inheriting the properties of the parent. Reproduction by the process of fission may be observed in many of the lower cryptogamous plants, and among animals in the infusoria, annelida, etc. What

Fig. 522.



Division of blood cells in embryo of stag. (Frey.)

Fig. 523.

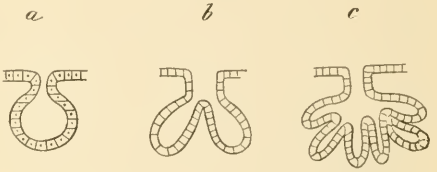


Hydroid colony. Eudendrium ramosum. (Gegenbaur.)

interests us in this connection, however, as regards fission is, that the segmentation of the vitellus of the egg, the development of the embryonic blood corpuscles (Fig. 522), the proliferation of the cells constituting morbid growths, etc., are accomplished by this process. On the other hand, by gemmation is understood the reproduction of the new being by a process of budding, as seen in ordinary flower-

ing plants, and among animals in the hydra, actinia, etc., each bud becoming a new animal. In certain cases of gemmiparous reproduction, however, the buds, instead of being cast off as produced, remain attached to the parent stock, and so give rise to a colony, as in the hydroids (Fig. 523), each member of which is in communication, directly or indirectly, with each other. Such a mode of reproduction in the human body is seen in the development of a compound gland (Fig. 524), through the division and subdivision of a simple follicular gland.

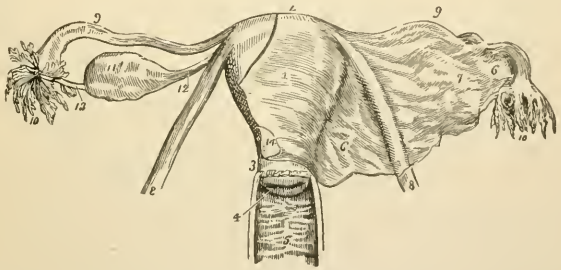
Fig. 524.



Diagrammatic view of development of glands.

The reproduction of man and most animals, however, is accomplished by the union of a spermatozoön and an ovum, both male and female generative organs co-existing, however, in the same individual in many invertebrates. In the tapeworm, for example, which is a hermaphrodite, reproduction is accomplished even by self-impregnation. The ova and spermatozoa are specialized products of the male and female generative apparatus respectively, which, while elaborated by a process of fission, unlike the products of the latter, must fuse together in order to give rise to a new being, neither spermatozoön nor ovum, by themselves being capable of further development. Further, it will be observed that since, in the production of a new being by sexual generation, the union of the spermatozoön and ovum is indispensable, the qualities of the parents must be transmitted to their offspring. The

Fig. 525.



Sketch of the uterus and its appendages. 1. Uterus, with its peritoneal covering partially retained. 2. Its fundus. 3. Its neck, with the forepart of the attachment of the vagina removed. 4. Mouth of the uterus. 5. Interior of the vagina. 6. Broad ligament, removed on the opposite side. 7. Position of the ovary behind the broad ligament. 8. Round ligament. 9. Oviduct, or Fallopian tube. 10. Its fimbriated extremity. 11. Ovary. 12. Ovarian ligament. 13. Process connecting the fimbriated extremity with the ovary. 14. Cut border of the broad ligament. (Wilson.)

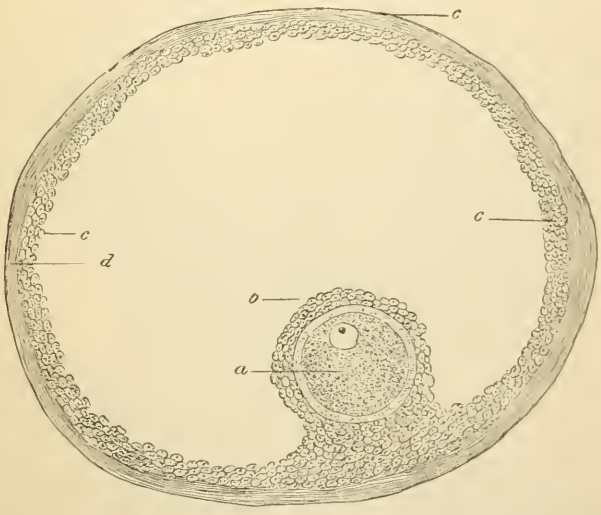
female generative organs, situated partly within and partly without the pelvis, consist of the uterus, Fallopian tubes, vagina, ovaries, the external and internal labia, clitoris, etc. The uterus (Fig. 525),

or womb, is a pyriform, hollow muscular organ, lying, in the unimpregnated condition, within the pelvis, between the rectum and the bladder, and maintained in position by its attachment to the vagina by the recto- and vesico-uterine peritoneal folds, and the round and broad ligaments. Its upper broad extremity is known as the fundus, or base, the narrow extremity the cervix, or neck, and the intervening portion as the corpus, or body. The uterus is about three inches in length, two inches in breadth, and one inch in thickness.

The walls of the uterus consisting of unstriated muscular tissue, being about one-half an inch in thickness, its cavity is but a narrow space. The latter is lined with a thin, soft, smooth, and ciliated mucous membrane of a pale red color, containing numerous tubular glands adhering closely to the underlying muscular tissue, there being no intermediate fibrous or submucous tissue, which becomes continuous with the mucous membrane of the Fallopian tubes and that of the neck of the uterus. The mucous membrane of the latter is of the squamous character, thicker and less soft than that of the body of the uterus, its glands being of the simple follicular kind and secreting a tenacious mucus, the latter in an inspissated condition, giving rise to the so-called ovula Nabothi. The uterine mucus, both of the fundus and cervix, is alkaline in reaction. The Fallopian tubes, or the horns of the uterus, are trumpet-shaped tubes about four inches in length, extending from the fundus outwardly above and beyond the ovary. The outer free extremity opening into the abdominal cavity expands into a funnel-shaped orifice, the pavilion, the margin of which, being fringed with a number of irregular processes, gives rise to its name of fimbriated extremity. One of the largest of these fringed processes, doubled so as to include a furrow, extends along the edge of the broad ligament to be attached to the ovary. The Fallopian tube is lined with ciliated mucous membrane, continuous through its interim or uterine orifice with that of the cavity of the fundus, and disposed in a longitudinal manner or as narrow folds. The tube itself consists of fibrous intermixed with unstriated muscular tissue, loosely invested by peritoneum. The small sac, often absent, attached by a long pedicle close to the fimbriated extremity, is the remains of the duct of Müller of the embryo, as we shall see presently. The vagina is a cylindrical canal about four inches in length and an inch and a quarter in breadth (in the virgin adult), extending from the uterus, the neck of which projects into it, to the vulva. The vagina consists of three coats, an outer fibro-elastic, a middle unstriated muscular, and an inner mucous; the epithelium of the latter is of the squamous kind, and is provided with numerous minute conical papillæ. In the virgin condition the lower orifice or entrance of the vagina is constricted by a crescentic or zone-like fold of the lining of the membrane, the so-called hymen. The latter is usually obliterated by sexual intercourse, childbirth, etc.; in some instances,

however, it is so strong that even impregnation may occur without its being ruptured. Its presence cannot, therefore, be taken as an evidence of virginity, or its absence of the contrary. The inner surface of the anterior and posterior walls of the vagina is roughened by folds, the wart-like eminences into which they are divided more particularly at the entrance of the vagina being known as the carunculæ myrtiformes. While, as just mentioned, the uterine mucus is alkaline in reaction, that of the vagina is decidedly acid. The two ovaries are compressed ovoid bodies, situated behind the broad ligament and enclosed by a pouch of the latter about an inch from the uterus, to which they are attached by the ovarian ligament. The ovary consists of a reddish spongy fibrous stroma, enclosed in a dense fibrous tunic, the tunica albuginea. Within the stroma of the ovary are found numerous vesicular-like bodies, varying from a microscopical size to the fourth of an inch in diameter, the Graafian follicles or vesicles, so-called after Regnerus de Graaf, their discoverer.[1] These vesicles (Fig. 526), which

FIG. 526.



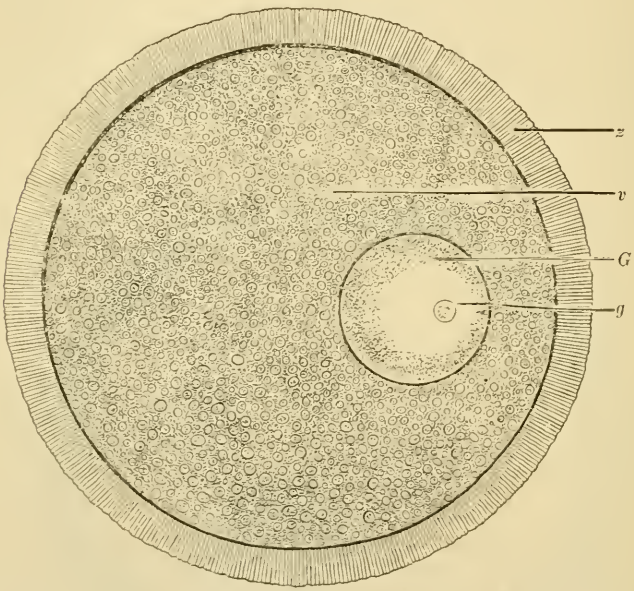
Ovum, Graafian follicle. *a*. Ovum. *b*. Discus proligerus. *c*. Membrana granulosa. *d*. Fibrous layer. (HAECKEL.)

are especially abundant at the peripheral portion of the stroma of the ovary, consist of an outer fibro-vascular layer or tunic, a middle basement membrane or membrana propria, and an inner layer of polyhedral granular epithelial cells, the membrana granulosa. At the side of the Graafian follicle lying next the surface of the ovary, the cells of the membrana granulosa are heaped up, constituting the discus proligerus, within which is found the ovum or

[1] De Mulierum Organis Generationi inservientibus Tractatus Novus, p. 177. Lugd. Batav., 1672.

egg, only discovered as recently as 1827 by Von Baer.[1] The remaining portion of the Graafian follicle—that is, the part not occupied by the discus proligerus with the enclosed egg—is filled with a serous liquid containing granules, nuclei cells apparently detached from the membrana granulosa. The ovum or egg, as just discharged from the follicle, has usually adhering to it the cells of the discus proligerus and shreds of epithelium; the latter being removed, the egg can then be seen with the naked eye on a perfectly clean piece of glass as a very minute speck, averaging in length the $\frac{1}{5}$ of a millimeter ($\frac{1}{120}$ of an inch) in diameter. Under the microscope the ovum or egg (Fig. 527) appears as a spheroidal body, ex-

Fig. 527.



The human ovum. *z*. Zona pellucida. *v*. Vitellus. *G*. Germinal vesicle. *g*. Germinal spot. (Haeckel.)

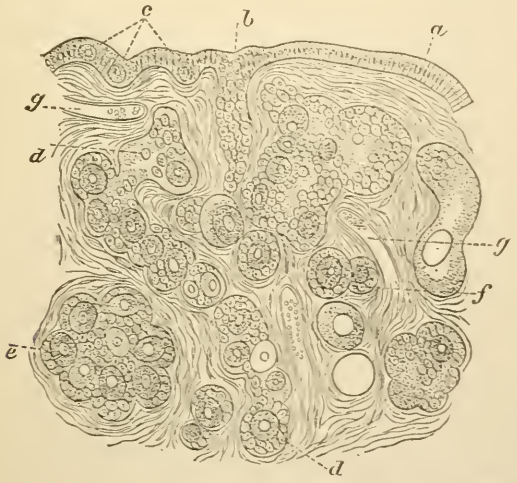
hibiting the characters of an organic cell as already described. Thus, it consists of a cell wall, an elastic membrane, the zona pellucida or vitelline membrane, measuring about $\frac{1}{100}$ of a millimeter ($\frac{1}{2500}$ of an inch) in diameter, and which, while apparently a clear pellucid membrane, is in reality striated, the striæ being possibly canals through which the spermatozoa pass into the egg.

The cell contents, yelk or vitellus, enclosed within the zona pellucida, consist of a soft or semi-fluid protoplasm or cytoplasm containing oil globules and yolk granules, among which may be clearly seen a nucleus and nucleolus. The yolk granules, or deutoplasm, being found in the greatest quantity in the middle of the ovum, are

[1] De Ovi mammalium et hominis generi, Lipsiæ, 1827. Ueber Entwicklungs Geschichte der Thiere, Königsberg, 1828.

often described as constituting the so-called deutoplasmic zone as distinguished from the clearer, more peripheral portion, the protoplasmic zone. The food, yolk, or deutoplasm exists only in small amount in the human ovum as the latter, being developed within the body of the mother and deriving its nourishment from the blood of the latter, but little is required for the early stages of growth. In this respect the ovum of the bird differs markedly from that of the human female, since the bird, being developed outside of the body of the mother, depends entirely upon the food yolk for its growth, hence the great amount present. The nucleus, or germinal vesicle, as it is called, in the ovum discovered in mammals by Coste,[1] in 1834, and usually situated near the surface of the egg is a clear, spheroidal vesicle, measuring about the $\frac{1}{150}$ of a millimeter ($\frac{1}{150}$ of an inch) and consists of protoplasm within which is found the nucleolus, macula, or the germinal spot. The latter, discovered by Wagner[2] in 1835, measures about the $\frac{1}{44}$ of a millimeter ($\frac{1}{3600}$ inch) in diameter. It may be mentioned in this connection that there is also found in most mammalian ova in the protoplasm a peculiar body, the so-called attraction sphere within which lies

FIG. 528.



Vertical section through the ovary of a newborn female. *a*. Ovarium epithelium. *b*. Egg string. *c*. Young ova. *d*. Egg string, with follicles. *e*. Follicles. *f*. Single follicle. *g*. Blood vessel. (WALDEYER.)

a single or double centrosome and which appears to initiate the karyokinetic division of the ovum to be presently described. It is a fact of profound significance that the human ovum, or first cell, from which all the cells composing the body are developed, should be practically undistinguishable, morphologically at least, from the

[1] Recherches sur la génération des Mammifères par Delpech et Coste. Paris, 1834.
[2] Müller, Archiv, 1835. Prodromus historiæ generationis. Lips., 1836.

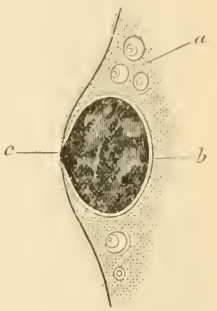
ova of the ordinary mammalia; that the first or transitory egg-stage through which man passes, should be permanently retained through life in many of the lower plants or animals, such beings never passing beyond the unicellular stage, and that the very lowest, as well as the highest forms begin life in exactly the same way as masses of protoplasm; the zona pellucida being a secondary formation. The ova are developed from the germinal epithelium (Fig. 528), a covering of the primitive ovary. Through the inward growth of this epithelium into the substance of the ovary, cords of cells (*b d*) are formed, which become divided into compartments through the encroachment of the fibrous stroma. Of the cells within these compartments the largest become ova; the smallest, the cells of the membrana granulosa of the Graafian follicle (*e f*), the wall of which is continuous with the stroma. As development advances, fluid accumulates between the growing cells, the follicle assumes the shape of a vesicle, the egg lying eventually to its inner wall. With the ripening of the ovum, the Graafian follicle comes to the surface of the ovary, the wall of which as well as that of the follicle becoming at the same time thinner and thinner, until, finally, they are ruptured, and so permit of the escape of the egg. From the fact of the egg or embryo being found in the Fallopian tube or uterus, except in the unusual case of abdominal pregnancy, it is evident that the Fallopian tube must be so disposed with reference to the Graafian follicle that at the moment of its rupture a temporary passage-way is usually formed from one to the other. As a matter of fact, it is not positively known how the egg passes from the Graafian follicle to the Fallopian tube. It may be supposed, however, that the fimbriated extremity affixes itself to the ovary at the moment of rupture of the follicle, or that the egg, dropping into the furrow of the long fimbriated process situated at the edge of the broad ligament and attached to the ovary, is transferred by ciliary action into the orifice of the tube, and thence by the same kind of action through the Fallopian tube into the uterus. The egg having arrived in the cavity of the latter, if not in the meantime impregnated, sooner or later decomposes and disappears. Before describing, however, the manner in which the ovum is impregnated, certain changes undergone by the Graafian follicle and the mucous membrane of the uterus, incidental to the maturation and escape of the ovum from the follicle, whether the ovum be impregnated or not, must be first considered.

Corpus Luteum of Menstruation and Pregnancy.

It is impossible to convey by words any idea of the extent of the congestion of the internal generative apparatus of the female during the period of the maturation and escape of the ovum from the Graafian follicle. The author can only say that in making post-mortem examinations of females dying while menstruating, he was impressed with the fact that the blood vessels, arteries, capillaries,

and veins were distended to an extent never accomplished by an artificial injection, however successfully performed. Such being the case (as might be expected) with the rupture of the Graafian follicle, there being quite an abundant hemorrhage, the cavity of the follicle fills with blood. The latter soon coagulating, as it would do if extravasated elsewhere, the clot remains enclosed within the walls of the follicle (Fig. 529), having no organic connection, however, with the latter, but simply lying loose in the cavity of the follicle, out of which it can be readily turned by the handle of a scalpel. The clot, which at this moment is large, soft, and gelatinous, soon begins to contract, and the serum exuded being absorbed by the adjacent parts, it becomes smaller and denser. The coloring matter of the clot at the same time undergoing the usual changes incidental to extravasation, and being to a great extent absorbed with the serum, a diminution in its color becomes quite perceptible. During this period, about two weeks, the lining membrane of the follicle, which at the moment of rupture presents a smooth, transparent, vascular appearance, becomes much thickened and convoluted. Through the continued condensation of clot and thickening of the lining membrane, as just described, the follicle has become so altered in its appearance that by the end of three weeks it can be no longer recognized as such, and is henceforth known as the corpus luteum, though its color can scarcely be said as yet to be distinctly yellow. At this period the corpus luteum may be described as a rounded tumor, about four-fifths of an inch (twenty millimeters) in length, situated in the stroma of the ovary, and projecting from the surface of the latter, the surface of the corpus presenting a minute cicatrix, the mark of the rupture of the follicle.

Fig. 529.

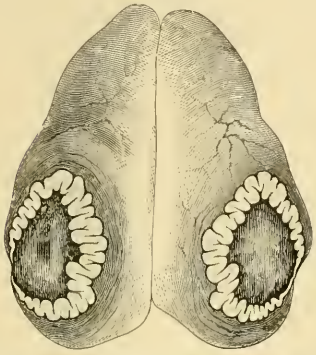


Graafian follicle, recently ruptured during menstruation, and filled with a bloody coagulum; shown in longitudinal section. *a*. Tissue of the ovary. *b*. Membrane of the vesicle. *c*. Point of rupture. (Dalton.)

If such a corpus luteum be divided longitudinally (Fig. 530), it will be found to consist of a central clot and the convoluted wall, and it will be observed that, while the clot and the convoluted wall lie in contact with each other, there is neither any organic connection between the convoluted wall and the clot, on the one hand, nor the surrounding ovarian tissues, on the other. From this time on, the corpus luteum undergoes a retrograde metamorphosis. By the end of the fourth week it is diminished to about half of the size attained at the end of the third week, the central clot has been, to a great extent, absorbed, the convoluted wall is with difficulty separated from the central clot and the peripheral ovarian tissue, and its color, instead of having faded, like that of the clot, is now a bright yellow. After this period it will be found impossible to separate

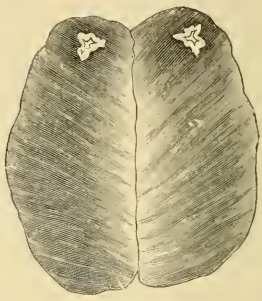
the yellowish convoluted wall, either from the ovarian tissue or the central clot, and by the end of two months the whole corpus luteum will be found to be reduced to the condition of a greenish, cicatrix-like spot (Fig. 531), about 6 millimeters (one-fourth of an inch) in

Fig. 530.



Human ovary cut open, showing a corpus luteum, divided longitudinally, three weeks after menstruation. From a girl, twenty years of age, dead of hæmoptysis. (Dalton.)

Fig. 531.



Ovary, showing corpus luteum, nine weeks after menstruation. From a girl dead of tubercular meningitis. (Dalton.)

diameter. At the end of six months the corpus luteum has usually disappeared. It may, however, be sometimes found, though in a very atrophied condition, even seven or eight months after the rupture of the follicle. Such, in brief, is the manner in which the corpus luteum of menstruation is developed out of the ruptured Graafian follicle from which the ovum has escaped, at least as observed by the author in a number of females dying from natural causes or violent deaths, and which does not differ essentially from the process so admirably described by Dalton.[1] As during pregnancy far more blood flows to the female generative apparatus than during menstruation, it might necessarily be supposed that while the production of the corpus luteum would be essentially the same in both conditions, the corpus luteum, being better nourished, would grow larger and persist longer than the corpus luteum of menstruation. That such is the case there can be no doubt, a corpus luteum being present at the end of pregnancy even, and measuring as much as half an inch in diameter. While marked differences exist, therefore, between the corpus luteum of menstruation and that of pregnancy, nevertheless, as these differences are of degree, and not of kind, and since the corpus luteum of menstruation during the first three weeks increases in size, but that of pregnancy after the first six months diminishes, it can be readily conceived that at a particular moment the corpus luteum of menstruation might be of the same size as that of pregnancy, and that if the color of the clot and convoluted wall in the two were not well marked,

[1] Trans. of the American Med. Assoc., Vol. iv., p. 547. Phila., 1851. Physiology, 7th ed., p. 608. Phila., 1882.

the two corpora lutea might be undistinguishable. At least such has been the experience of the author, in comparing numerous corpora lutea of menstruation of various ages with those of pregnancy. Further, that the presence or absence of a corpus luteum cannot be accepted as positive evidence of impregnation having taken place is shown by the fact that, although in several instances in making post-mortem examinations a fœtus was removed from the uterus by the author, not a trace of a corpus luteum could be found in either ovary, and, on the other hand, in more than one instance a well-developed corpus luteum being present several months after the last menstruation, there was not the slightest reason to believe that during that period there had been a fœtus in the uterus, at least the relatives of the deceased had no object in concealing the fact of impregnation, if such had really occurred.

Menstruation.

Coincident with the maturation and escape of the ovum from the Graafian follicle, the mucous membrane of the uterus undergoes several well-marked changes. Thus, while in the ordinary conditions it measures only about 18 millimeters ($\frac{1}{14}$ of an inch) in thickness, at this period it becomes twice or even three times as thick. It is also much softer and more loosely attached to the underlying part than ordinary, being somewhat rugose in character. The glands are very much enlarged, and the surface of the membrane smeared with blood. The latter is due to a kind of disintegration set up in the mucous membrane involving the blood vessels, by which the capillaries are ruptured. The hemorrhage so caused constituting the menstrual flow, or the menses, catamenia, etc., appears monthly in the healthy female, and lasts upon the average from four to five days. It appears to be pure arterial blood mixed with desquamated utero-vaginal epithelium; the amount of the latter would appear from the observations of the author to be greater than usually supposed. The menstrual blood is kept from coagulating by the vaginal mucus. As might be expected from the nature of the case, it is impossible to say how much blood is discharged during the menstrual period, for, apart from the difficulty experienced in collecting it, women vary very much in respect to the amount of blood lost. From 100 to 200 c.c. (4 to 8 ounces) may be accepted as an approximate estimate of the total flow during the menstrual period. Menstruation is sometimes regarded as the effect of ovulation, the two being so intimately associated. Since menstruation, however, occurs without ovulation in the absence of ovaries, and ovulation without menstruation, it is evident that the two phenomena are not related as cause and effect, but should be considered as the effects of a common cause, the general preparation of the system for impregnation. Indeed, the thickening and shedding of the mucous membrane of the uterus, and hemorrhage during menstruation, differ only in degree, not in kind, from

the changes undergone by the mucous membrane during pregnancy and parturition, the decidua menstrualis being the forerunner of the decidua graviditatis. That the menstrual flow is the effect of a deeply-lying cause, the fitting of the mucous membrane for the reception of the ovum, though not due to the production of the latter, is shown by the constitutional disturbance experienced by the female when the menses first appear, and ever afterward with their monthly reappearance, though then to a less extent. The menses usually appear between the age of thirteen and fifteen years and much earlier in warm climates. At this period, the age of puberty, there is a general development of the body, the limbs become fuller and rounder, hair appears on the mons veneris, the mammary glands enlarge, ova maturate, and the disposition changes. Just before the establishment of the flow, either in the case of its first appearance or in after-recurring ones, for about two days a feeling of general malaise is experienced, particularly a sense of weight and fulness in the pelvic organs, the vaginal mucus is increased in amount and becomes rusty in color, and gives rise to the odor so perceptible in certain females, the breasts also enlarge, showing the sympathy existing between the latter and the generative organs. With the establishing of the flow, the disagreeable feelings and uneasiness usually pass away, and by the end of the fourth day, though the time varies, the flow ceases, and the mucous membrane returns to its normal condition. At about forty-five years of age the menses become irregular in their recurrence and usually cease altogether at fifty. The phenomenon of the menses is not restricted to the human female, as is often supposed, the heat or rut of the lower domestic animals, such as that of the mare, cow, bitch, being essentially the same process, only recurring at different intervals. Indeed, in monkeys and apes there is a monthly discharge, as in the case of the human female. It is a significant fact that the female of animals, except monkeys, only receive the male during the rutting or menstruating period.

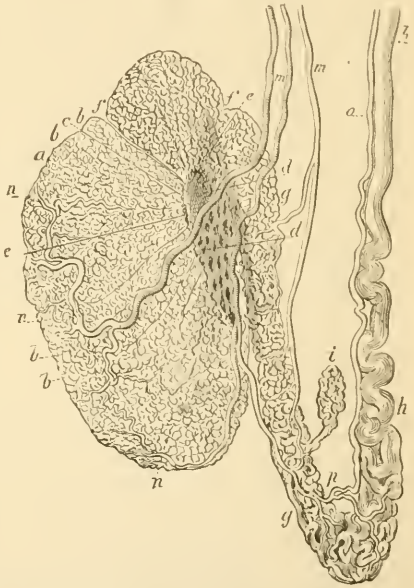
The Male Generative Apparatus.

The male generative apparatus consists of the testicles, the spermatic ducts, the seminal vesicles, prostate and suburethral glands, and the penis. The testicles (Fig. 532), secreting the spermatic fluid, are two glandular bodies suspended by the spermatic cords within the scrotum. The latter is essentially a musculocutaneous pouch, divided into two recesses by a septum for the reception of the two testicles. Each testicle consists of an anterior oval portion of the body, or testis proper, and a posterior elongated portion clasping, as it were, the former, the epididymis. The upper portion of the epididymis is known as the head, or globus major, the lower part as the tail, or globus minor, which, in turning upward upon itself, becomes the spermatic duct. The testes are covered with a dense white fibrous membrane, the tunica albuginea, which

at the back of the testes forms a process, the mediastinum. The latter, being prolonged as fibrous bands to be inserted into the inner surface of the tunica albuginea, serves as a sort of scaffolding to support the delicate glandular substance within. The testicle proper is made up of about two hundred lobules, each lobule in turn consisting of from one to six seminiferous tubules, of which there are perhaps eight hundred in all.

The seminiferous tubules at the narrow end of the lobule assume a straight course, being then known as the vasa recti. The latter entering the mediastinum, constitute together the plexus retiformis, from which emerge about a dozen efferent canals, or vasa efferentia, to pass out to the head of the epididymis. Within the latter these efferent canals form the spermatic cones, which finally give rise to one convoluted tube, constituting the body and tail of the epididymis, the latter of which, as just mentioned, becomes the spermatic duct. The spermatic duct passing through the inguinal canal, leaves the latter at the internal abdominal ring, and descending backward and downward, passes forward to form, together with the duct of the seminal vesicle, the ejaculatory duct, the latter terminating in the prostatic urethra. The seminiferous tubules, about thirty inches in length when unravelled, and the $\frac{1}{120}$ of an inch in diameter, consist of a fibro-membranous wall lined with a delicate layer of soft polyhedra nucleated cells, the sperm cells, which elaborate the spermatic or seminal liquid, of which about half a drachm is emitted during the orgasm. The latter is a faintly alkaline liquid, slightly heavier than water, becoming jelly-like first, and then hardening after emission. The semen consists chemically of 82 per cent. water, serum, albumin, alkali albuminate, nuclein, lecithin, cholesterin, fats, phosphorized fats, alkaline, and earthy phosphates, sulphates, carbonates, and chloride, and an odorous body, the so-called "spermatin," the nature of which is unknown.

FIG. 532.

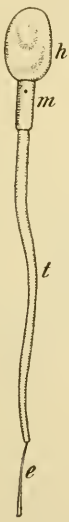


Testicle and epididymis of the human subject. *a*. Testicle. *b*. Lobules of the testicle. *c*. Vasa recta. *d*. Rete testis. *e*. Vasa efferentia. *f*. Cones of the globulus major of the epididymis. *g*. Epididymis. *h*. Vas deferens. *i*. Vas aberrans. *m*. Branches of the spermatic artery to the testicle and epididymis. *n*. Ramification of the artery upon the testicle and epididymis. *o*. Deferential artery. *p*. Anastomosis of the deferential with the spermatic artery. (KÖLLIKER.)

Physiologically the essential portion of the spermatic fluid, upon which its fecundating powers without doubt depend, are the spermatozoa that it contains. Indeed, if the seminal liquid be deprived of its spermatozoa, it is rendered entirely inoperative as regards impregnation.

The spermatozoa are developed out of the nuclei of the daughter cells of the parent cells, which lie near the outer wall of the seminiferous tubule, the nucleus assuming the form of a spermatozoön, which is set free by the deliquescence of the cell wall enclosing it. The spermatozoa appear first at the age of puberty, and afterward till the end, life being found in the semen of healthy men of ninety years of age. The spermatozoa (Fig. 533), measuring the $\frac{1}{2\,4}$ of a millimeter ($\frac{1}{6\,0\,0}$ inch) in length, discovered by Von Hammen, in 1677, and described by Leeuwenhoek, resemble the flagellate animalculæ for which they were first taken. A spermatozoön consists of an ovoidal head, measuring $\frac{1}{2\,4\,0}$ of a millimeter ($\frac{1}{6\,0\,0\,0}$ of an inch) containing chromatin and of a filamentary appendage or tail measuring 0.050 mm. ($\frac{1}{5\,0\,0}$ of an inch) which vibrates with astonishing rapidity. The tail of the spermatozoön is usually described as consisting of three parts, the middle, main, and end pieces. The middle piece or the thickest part, that nearest the head, is said to contain an axial thread and exhibits a very fine spiral thread running around it. The movements of the spermatozoa are arrested by water and cold, retarded by acids, and favored by alkalies. The spermatic fluid, with the spermatozoa, passes from the testicles by the spermatic ducts to the seminal vesicles, where it becomes mixed with the secretion of the latter, the nature and use of which are, however, doubtful, as no secreting glands are found in these vesicles; its use may be to dilute the mixed spermatic fluid. The spermatic fluid, having accumulated in the seminal vesicles, is thence introduced during coition, still further mixed with the secretion of the prostate gland, of the glands of Cowper, and of the urethra, the use of which is not known, by an ejaculatory effect, into the vagina of the female, the spermatozoa by their vibrating movements passing up into the Fallopian tubes, and even the ovaries, as shown by the development of the ovum in those situations in cases of extra-uterine pregnancy. The spermatozoa have been found moving in the uterus even eight days after emission, the rate of movement being probably from between 1.2 to 3.6 mm. per minute. In order that coition should be accomplished, it is essential that the penis should be erect. This is brought about through its blood supply being very much increased by the stimulation of the vaso-dilator

FIG. 533.



Human spermatozoön. *h*. Head. *m*. Middle-piece. *t*. Tail. *e*. End-piece. (RETZIUS.)

fibers of the nervi erigentes, the later arising probably from the second sacral nerves. The center of erection, situated in the cord, can be reflexly stimulated either by impressions made upon the genital organs or upon the mind. The ejaculatory effort is due to the simultaneous contraction of the bulbo urethræ, ischio-cavernous, and transverse perinæus muscles, due to the reflex stimulation of the ejaculatory center of the spinal cord, situated in the lumbar region.

Recent researches[1] render it probable that the testicles, in addition to secreting the spermatic fluid, elaborate an "internal secretion," spermin,[2] having a chemical composition represented by the formula $C_5H_{14}N_2$, and which, passing into the blood, increases the mental and physical vigor of the aged, and benefits those afflicted with general prostration and neurasthenia.[3]

[1] Brown-Sequard, Archives de Physiologie normale et pathologique, 1889, 92.
[2] Poehl, Zeitschrift für klinische medecin, Band 26, 1894, s. 133.
[3] Zoth, Pflüger's Archiv, Band 62, 1896, s. 335. Preyer, Ibid., s. 379.

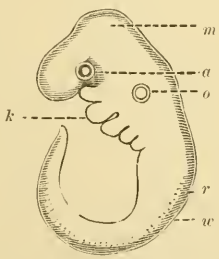
CHAPTER XLVI.

REPRODUCTION.—(*Concluded.*)

Impregnation of the Ovum and Development of Embryo.

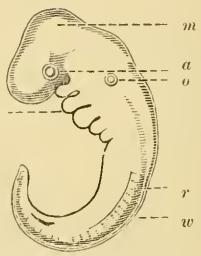
As a matter of fact, nothing is known as to the manner in which the ovum is impregnated in the human female, or of the early stages of the development of the embryo. Since the primitive ova of all animals are more or less alike and the spermatozoa differ from each other unessentially, it is to be inferred that the process of impregnation in the human female is the same as that observed in animals. Further, as the human fœtus of about three weeks old (Fig. 534)

FIG. 534.



Embryo of man.

FIG. 535.



Embryo of rabbit.

a. Eye. *m*. Mid-brain. *o*. Ear. *r*. Spinal marrow. *w*. Vertebral column. *k*. Visceral arches. (HAECKEL.)

differs but little from that of the rabbit at about ten days (Fig. 535), there can be little doubt that the stages intermediate between that of the egg and that of three weeks old, through which the human embryo passes, are essentially the same as the corresponding stages through which the rabbit embryo passes from the stage of the egg to that represented in Fig. 535, or the corresponding stages in the development of the dog, hog, etc., or even bird, reptile, or fish. Assuming, then, that the development of man, in the early stages, is the same as that of a rabbit, for example, we will describe, as illustrating the former, the development of the animal[1] up to the period that it begins to differ from that of man, basing our account of impregnation, however, upon the manner in which that process is said to take place in the Ascaris megalocephala,[2] a large worm found in the alimentary canal of the horse.

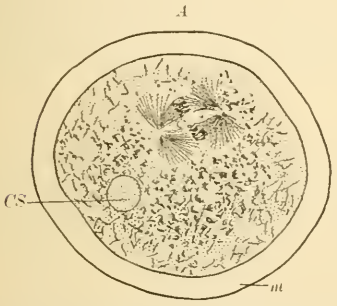
[1] Bischoff, Entwicklungs Geschichte des Kaninchen-Eies. Braunschweig, 1842. E. Van Beneden, La Maturation de l'œuf, etc., d'apres des recherches faites chez le lapin. Bruxelles, 1875.

[2] Van Beneden et Neyt, Nouvelles recherches sur la fécondation et la division mitosique chez l'ascaride mégalocéphale, Bullet. de l'acad. royale des sciences de Belgique, 3 ser., T. xiv., 1887.

Either before or immediately after its escape from the Graafian follicle the ovum undergoes a change known as "maturation," a process preparatory to, but independent of fertilization. This consists in the extrusion by the germinal vesicles of two minute spherical bodies, the "polar globules" or "directive corpuscles," so-called on account of it being supposed by some embryologists that their presence determinates the pole at which the first segmentation will take place in the event of the ovum being impregnated. The polar globules are formed in the ovum of the Ascaris megalocephala[1] in the following manner:

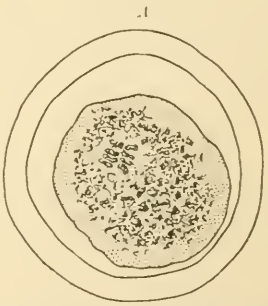
The germinal vesicle approaches the periphery of the vitellus, becomes indistinct in outline, and is transformed into a spindle of fibers, at the equator of which are situated eight chromatin particles (Fig. 536). The latter shortly separate into two sets, consisting of four chromatin particles each (Fig. 537). One set of four

FIG. 536.



The ovum, with the germinal vesical transformed into a spindle of achromatic fibrils; from the poles of the spindle other fibrils radiate into the protoplasm. At the equator of the spindle eight portions of chromatin are visible. *CS*. Head of a spermatozoön which has previously entered the ovum, and is becoming transformed into the male pronucleus. *m*. Gelatinous membrane of the ovum. (QUAIN.)

FIG. 537.



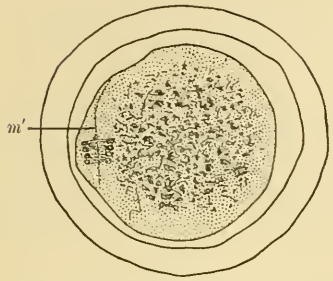
The chromatin particles are seen separated into two sets. The achromatic fibrils are not shown in this preparation. The ovum is considerably shrunken. (QUAIN.)

chromatin particles, together with part of the protoplasm, is extruded into the peri-vitelline space as the first polar globule (Fig. 538), while the other set of four chromatin particles remains in the vitellus situated upon the equator of the second spindle into which the remainder of the germinal vesicle has been transformed (Fig. 539). Soon two chromatin particles are extruded from the spindles as the second polar globule (Figs. 540, 541), while the other two chromatin particles remain in the vitellus and constitute, with the remainder of the germinal vesicle, the female pronucleus. The act of impregnation in the rabbit, and in all animals in which impregnation has been observed, consists in the passage of one or more spermatozoa (Fig. 542) through the vitelline membrane of the egg into the peri-vitelline space, though one spermatozoön alone normally enters the vitel-

[1] Gehuchten Nouvelles observations sur la vésicule germinative et les globules polaires de l'Ascaris Mégalocéphale, Anat. Anz., 1887.

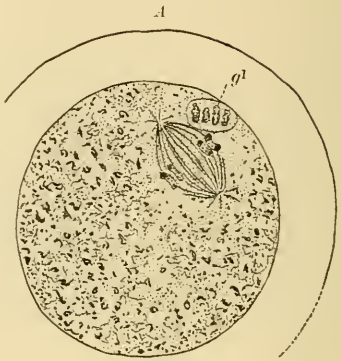
lus to form the male pronucleus, the union of which with the female pronucleus gives rise to the new being.

Fig. 538.



Half of the germinal vesicle is extruded into a peri-vitelline space, and along with a portion of the protoplasm is becoming separated off from the ovum as a polar globule. The extruded half includes four of the chromatin particles; the other four remain in the ovum. m'. Membrane dividing the polar globule from the ovum. (QUAIN.)

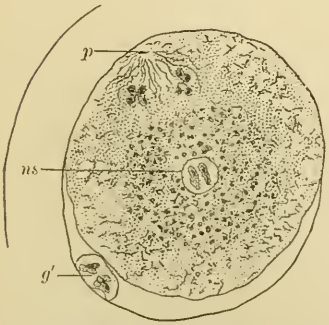
Fig. 539.



The remainder of the germinal vesicle (after extrusion of the first globule g^1) has again become transformed into a spindle of achromatic fibrils, with the four remaining chromatin particles at the equator of the spindle. (QUAIN.)

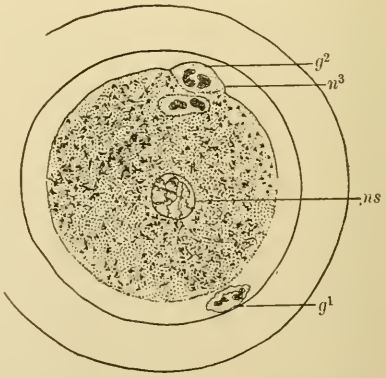
It has also been shown that the head of the spermatozoön, which is the part that is transformed into the male pronucleus, contains only two chromatin particles, the other two having been thrown off in

Fig. 540.



The spindle p, now irregularly Y-shaped, is seen approaching the surface of the ovum. g'. First polar globule. ns. Male pronucleus which has become formed from a spermatozoön. (QUAIN.)

Fig. 541.

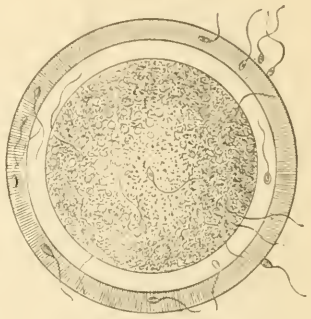


Completion of the process. The second polar globule, g^2, is now separated from the ovum; it contains two of the chromatin particles. The other two remain in what is left of the germinal vesicle. n^3. Which now forms the female pronucleus. ns. Male pronucleus. g^1. First polar globule. (QUAIN.)

the "maturation" of the spermatozoön during its development from the nucleus of the daughter cell of the parent cell of the seminiferous tubule. It would appear, therefore, that through the formation of

the polar globules as just described, room is made, so to speak, for the reception by the female pronucleus of the two chromatin particles brought to it by the male pronucleus, the original number of chromatin particles, viz. four, being, therefore, restored by the union of the female and male pronucleus. However that may be, the formation of the polar globules appears to be an indispensable condition to the impregnation and further segmentation of the ovum. The two chromatin particles of each of the two pronuclei are now transformed into a skein (Fig. 543), the two pronuclei being separated by the two so-called "attraction bodies" which appear at this stage of development. The skeins eventually assume the shape of four V-shaped loops or filaments (Fig. 544), and which are distinctly visible even after the conjugation or union of the two pronuclei. As development advances the V-shaped chromatin particles split longitudinally (Fig. 545).

FIG. 542.



Passage of spermatozoa into ovum. (HAECKEL.)

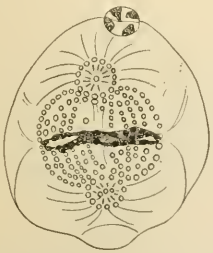
FIG. 543.

The chromatin filaments of the pronuclei have become transformed into skeins. Two attraction-spheres, each with a central particle, united by a spindle of achromatic fibers, have made their appearance near the pronuclei. The male pronucleus has the remains of the body of the spermatozoön adhering to it. (QUAIN.)

FIG. 544.

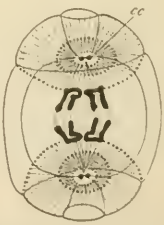
The V-shaped filaments are splitting longitudinally. The attraction-spheres and achromatic spindles, although present, are not shown. (QUAIN.)

FIG. 545.



Equatorial arrangement of the four chromatin loops in the middle of the now elongated ovum; the achromatic substance forming a spindle-shaped system of granules with fibrils radiating from the poles of the spindle (attraction-spheres) into the protoplasm, commencing division of the ovum into two cells. (QUAIN.)

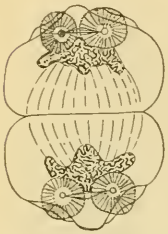
FIG. 546.



Further separation of the chromatin filaments. Each of the central particles of the attraction-spheres has divided into two. (QUAIN.)

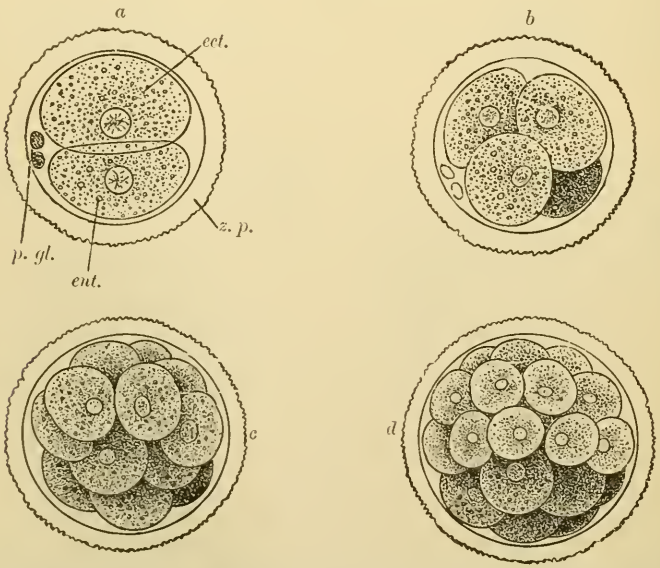
and dispose themselves for a time along the equator of the spindle-shaped nucleus, four of the chromatin filaments passing soon upwards towards one pole and four towards the other (Fig. 546). Finally the chromatin filaments are transformed into the skeins of the daughter nuclei developed through segmentation, each attraction sphere dividing at the same time into two (Fig. 547). The process of segmentation, that is the cleavage or furrowing of the vitellus, begins shortly after the formation of the new nucleus, the division of the vitellus (which has shrunk away from the vitelline membrane) into two new spheres, being preceded by the formation of a spindle-shaped system of achromatic fibrils, such as take place in the karyokinesis or mytosis of an ordinary cell.[1] The two spheres (Fig. 548, *a*), so formed by fission, subdividing into four (Fig. 548, *b*), and the four into eight, the eight into sixteen (Fig. 548, *c*), and so on, the original single vitellus becomes finally

Fig. 547.



The daughter nuclei exhibit a chromatin network. Each of the attraction-spheres has divided into two, which are joined by achromatic fibers, and are connected with the periphery of the cell in the same manner as the parent sphere. (Quain.)

Fig. 548.

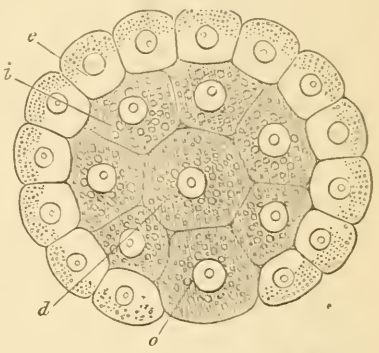


First stages of segmentation of a mammalian ovum; semi-diagrammatic. *z. p.* Zona pellucida. *p. gl.* Polar globules. *a.* Division into two segments. *a.* Larger and clearer segment. *l.* Smaller, more granular segment. *b.* Stage of four segments. *c. d.* Succeeding stages of segmentation showing the more rapid division of the clearer segments and the enclosure of the darker segments by them. (Quain.)

[1] It may be mentioned in this connection that, according to the modern investigations of Butschli, Hertwig, Strasburger, etc., cells appear to be generally reproduced by karyokinesis rather than by simple fission.

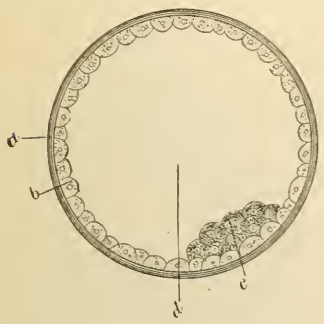
transformed into a mulberry-like mass of vitelline spheres (Fig. 548, *d*), the vitelline membrane remaining, however, undivided. These cells are not of the same size and are differently affected by reagents. The larger cells arrange themselves in the center, the smaller ones at the periphery and in a single row, the latter enclosing the former, as a cup, its contents. The egg now reaches its gastrula stage (Fig. 549). Shortly afterward, however, through one of the larger inner cells being drawn inward, the mouth (*o*) of the gastrula disappears, and the latter now forms a ball consisting of large cells within and covered by a single layer of small vesicles without. Fluid, formed probably through the deliquescence of some of the cells, appears between the inner cells and the layer of outer ones; the latter is expanded into a one-layered globular vesicle, the inner cells remaining as a ball of cells adhering to the outer layer at a point where the mouth of the gastrula was situated. The inner cells now lose their ball-like form, and becoming flattened, assume a discoidal shape, spreading themselves out. The gastrula, so modified, is now known as the blastodermic vesicle (Fig. 550), and consists, as shown in section, of the original zona pellucida or cell-wall (*a*) which we shall henceforth

Fig. 549.



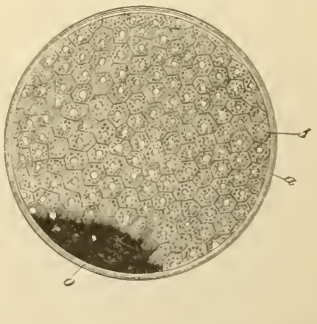
Gastrula of rabbit, in longitudinal section. (Haeckel.)

Fig. 550.



Blastodermic vesicle of rabbit, seen in section. (Haeckel.)

Fig. 551.



Blastodermic vesicle of rabbit, seen from surface. (Kölliker, after Bischoff.)

designate as the chorion, of a single layer of cells (*b*) lying next to the chorion and constituting the wall of the blastodermic vesicle, of a heap of cells (*c*) adhering to the inner surface of the wall. The latter being darker in color than the cells forming the wall of the

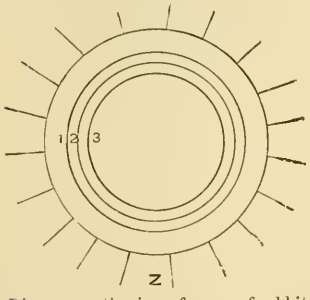
vesicle, looks like a dark mass when the blastodermic vesicle is viewed from the surface, the cells of the wall then appearing like a mosaic (Fig. 551).

The changes just described by which the egg is transformed into the blastodermic vesicle appear to take place as the egg passes through the Fallopian tube.

Formation of Blastodermic Membrane.

The blastodermic vesicle does not remain, however, long a one-layered vesicle, but soon, through the extension of the disk-like dark cells around to the opposite pole of the egg, a two-layered vesicle; and further, through development of a third layer intermediate between the external and internal one, a three-layered vesicle (Fig. 552), not including, of course, the chorion (Z) or the original zona pellucida of the egg, which now presents here and there over its outer surface little wart-like villous processes. The three layers of which the blastodermic vesicle now consists (1, 2, 3, Fig. 552) are known from without inward as the external, middle, and internal blastodermic membranes, or, more briefly, as the epiblast, mesoblast, and hypoblast.

Fig. 552.

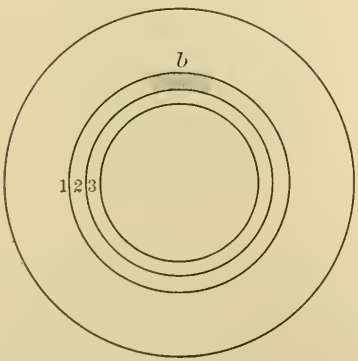


Diagrammatic view of ovum of rabbit, consisting of chorion, enclosing three-layered blastodermic vesicle.

Development of Primitive Organs.

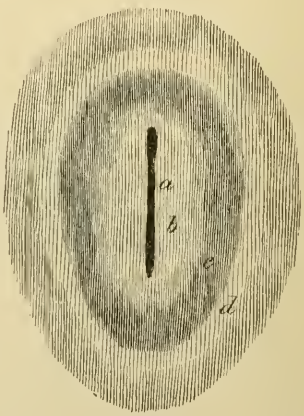
Shortly after the development of these three layers through the thickening of the two outer ones (Fig. 553, *b*), there appears

Fig. 553.



Diagrammatic view of ovum of rabbit to show formation of germ shield *b*.

Fig. 554.



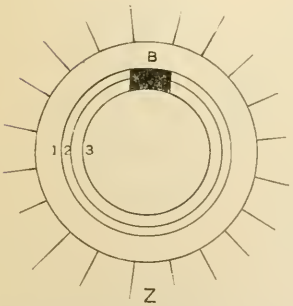
Germ shield of rabbit (*b*). Primitive groove (*a*). Area pellucida (*c*). Area opaca (*d*).

within tolerably well-defined limits an opaque oval-like body, the so-called "double shield,"[1] "embryonic area,"[2] or germ shield[3] and which indicates the rudiment more particularly of the dorsal portion of the body of the future embryo, the remaining portions of the blastodermic membranes not entering into the formation of the body of the embryo, but appropriated, as we shall see presently, for the formation of the true and false amniotic folds and umbilical vesicle. If the blastodermic vesicle be viewed, not in section, but from the surface, the germ shield will be seen (Fig. 554, *b*) as an oval-like structure, lying in the center of a pellucid area (*c*), so called on account of the latter being surrounded by an opaque area (*d*), the whole area extending from edge to edge of the area opaca (*d*), being known as the area germinativa, which at this period, while oval-shaped, is at its first appearance round in form.

Shortly after the development of the germ shield there appears along its central line a delicate white streak, the primitive streak[4] or axis plate,[5] due to the coalescence of the three blastodermic membranes along the middle line, as shown by section (Fig. 555, B), and with further development within the latter a delicate groove or furrow, the primitive groove, which, however, soon disappears. Its function is unknown.

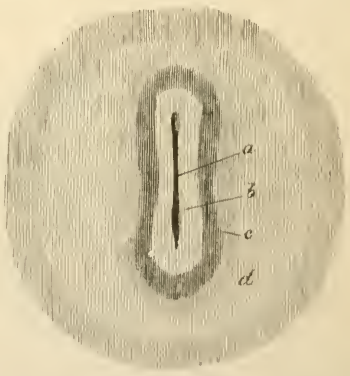
Shortly after the development of the primitive groove there appears a second groove (Fig. 556, *a*) situated in front of the former, the medullary groove, so called on account of it giving rise through the closing in of its walls, or the medullary folds, along the middle line to the primitive medullary tube, or central nervous system. As the

FIG. 555.



Diagrammatic view of ovum of rabbit to show formation of primitive streak (B) by fusion of blastodermic membranes.

FIG. 556.

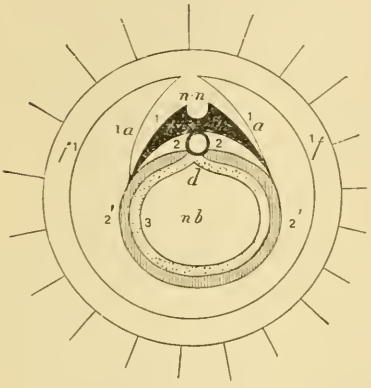


Lyre-shaped germ shield of rabbit. *a*. Medullary groove. *b*. Germ shield. *c*. Area pellucida. *d*. Area opaca.

[1] Remak, Untersuchungen über die entwickelung der Wirbelthiere, s. 7. Berlin, 1855. [2] F. M. Balfour, Treatise upon Comparative Embryology, Vol. ii., 1881, p. 180.
[3] Haeckel, Anthropogenie, Vierte Auflage, 1891, s. 285.
[4] Von Baer, Ueber Entwickelungs Geschichte der Thiere. Zweiter Theil., s. 69, s. 190. Königsberg, 1887. [5] Remak, op. cit., s. 7.

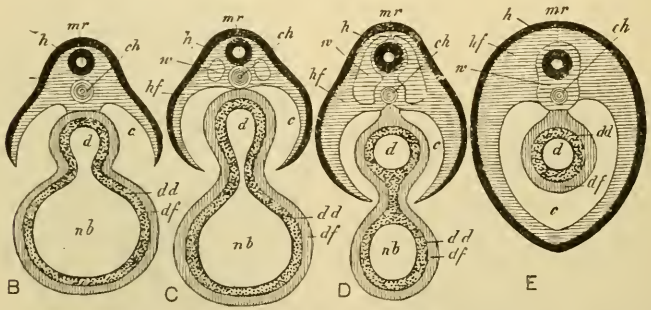
medullary groove (*a*) deepens, the germ shield (*b*) and area pellucida (*c*) lose their oval shape and become lyre- or sole-shaped, the area opaca (*d*), however, reassumes its original round shape. Returning now to the consideration of the embryo as more advanced in development, it will be seen that not only the medullary groove or furrow (Fig. 557) is much deepened, but that the external blastodermic membrane rises up into folds (1*a*), which, arching over the dorsal surface of the embryo, coalesce in the middle line and form the amnion, the remaining portion of the external blastodermic membrane receding from the amnion proper as the false amniotic folds (*f'*), until they finally fuse with the inner surface of the chorion. It will also be observed that the middle blastodermic membrane or mesoblast has split into two layers (Fig. 558, *hf* and *df*), of which *hf*, the skin fibrous layer, unites with the skin sensory layer *h*, to form the somatopleure or the parietes of the body, while the intestinal fibrous layer *df*, in adhering to the hypoblast *dd*, forms the splanchno-

FIG. 557.



Diagrammatic view of ovum of rabbit to show medullary furrow, amniotic folds, splitting of mesoblast.

FIG. 558.



In all the figures the letters indicate the same parts. *h*. Skin sensory layer. *mr*. Spinal tube. *hf*. Skin fibrous layer. *w*. Primitive vertebræ. *ch*. Notochord. *c*. Body-cavity (*cœloma*). *df*. Intestinal fibrous layer. *dd*. Intestinal glandular layer. *d*. Intestinal cavity. *nb*. Umbilical or vitelline vesicle. (HAECKEL.)

pleure, or the fibro-muscular wall of the primitive alimentary canal and umbilical vesicle, the space between the two layers of the mesoblast C becoming eventually the cœlom or primitive body cavity, while the internal blastodermic membrane, or the intestinal glandu-

lar layer *d d*, giving rise only to the mucous membrane lining the same. An inspection of these different sections will show also that just as the primitive neural canal, or spinal cord, is developed through the medullary groove (*mr*) being transformed into a tube, which later becomes entirely separated from the external blastodermic membrane, the latter giving rise to the epithelium or epidermis of the skin, so through the deepening of the furrow (*d*) in the internal blastodermic membrane the primitive alimentary canal is formed, the umbilical vesicle, originally part of the same, being constricted off by the bending downward and inward of the parietes of the body.

An inspection of Fig. 558 will also show that as the medullary groove or spinal tube (*mr*) of the external blastodermic membrane is formed there is developed within the internal blastodermic membrane a rod of cartilage (*ch*), the notochord, or chorda dorsalis, which represents the axis around which will be developed the bodies of the future vertebræ, the neural canal being finally enclosed by a bony spinal canal, through ossification of that portion of the mesoblast lying above and on either side of the notochord. The embryo of the rabbit consists at this period, then, apart from the enveloping chorion (Fig. 558, E), of two tubes, a neural one above, an alimentary tube below, separated by a rod of cartilage, and enclosed by the walls of the body, the space between the two layers of the mesoblast representing the cœlom, or body cavity. Resuming what we have just endeavored to describe, it will be seen that through the process of segmentation the vitellus is transformed into a mass of cells, that these cells dispose themselves as three membranes or layers, that the three layers give rise to the primitive organs of the body, out of which the remaining organs are developed, as follows :

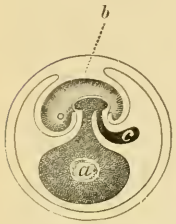
MEMBRANES AND LAYERS OF EMBRYO AND ORGANS DEVELOPED FROM THEM.

Membranes.	Layers.	Organs.
External blastodermic membrane or epiblast,	Skin, sensory,	Epidermis. Central nervous system. Primitive kidneys.
Middle blastodermic membrane or mesoblast,	Skin, fibrous,	Dermis. Peripheral nervous system. Osseous " " Muscular " " Testes.
	Intestinal fibrous,	Vascular system. Mesentery. Wall of alimentary canal and appendages. Ovaries.
Internal blastodermic membrane or hypoblast,	Intestinal glandular,	Epithelium of alimentary canal and appendages. Notochord.

Development of Amnion, Allantois, and Umbilical Vesicle.

It has already been mentioned that that portion of the external blastodermic membrane not entering into the formation of the embryo rises up into folds (Fig. 559) at the sides, head, and tail ends

Fig. 559.



a. Umbilical vesicle. *b*. Amniotic cavity. *c*. Allantois. (Dalton.)

Fig. 560.

Fecundated egg, with allantois nearly complete. *a*. Inner lamina of amniotic fold. *b*. Outer lamina of ditto. *c*. Point where the amniotic folds come in contact. The allantois is seen penetrating between the inner and outer laminæ of the amniotic folds. (Dalton.)

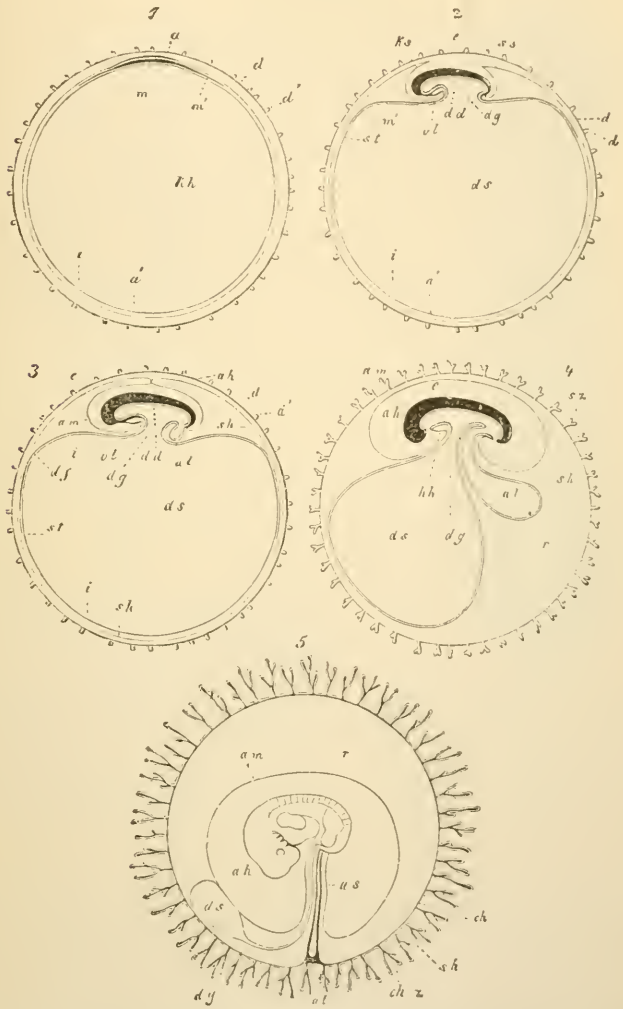
Fig. 561.

Fecundated egg, with allantois fully formed. *a*. Umbilical vesicle. *b*. Amnion. *c*. Allantois. (Dalton.)

of the latter, and arching over its back, and coalescing in the middle line, form the amnion (*a*), the remaining peripheral portions of the extensive blastodermic membranes not giving rise to the amnion receding as the false amnion (*b*) from the true one (Fig. 560), until it reaches the inner surface of the chorion, with which it ultimately fuses. It will also be seen from Fig. 559, that during the formation of the amnion (*b*) there buds out as an outgrowth of the posterior portion of the intestine a vesicle, the allantois (*c*), which, growing outward, gradually extends itself (Fig. 560), around the entire inner surface of the chorion, the cavity of the vesicle being finally obliterated by the fusion of its outer and inner layers (Fig. 561). The chorion, covered with villous processes (Fig. 562, 5 *ch* 2) at this stage will consist, then, from without inward, of the original zona pellucida of the false amnion, the allantois. As the allantois develops, blood vessels make their appearance in it, derived from the vessels of the fœtus, as we shall see presently, which, in extending into the villous processes of the chorion, serve to convey to the fœtus the nutritive material introduced by osmosis from the uterine blood of the mother, the allantois constituting, in fact, the fœtal part of the placenta. With the establishing of the allantois, and the consequent nourishing of the fœtus by the mother, the umbilical vesicle (Fig. 562, *d s*), which, up to this time, through its vessels, nourished the same, begins now to diminish in size, and finally disappears altogether. As the human embryo, at the earliest period of its existence, so far as observed—that is, from about twelve to fourteen days old—consists, essentially, of the same primitive organs and appendages as that of the rabbit, there can be no

doubt that the still earlier stages of its development, not yet actually seen, are essentially the same as those just described as taking place in the rabbit.

FIG. 562.

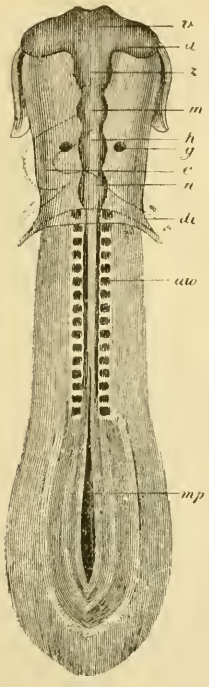


Diagrammatic figures, illustrating the development of the mammalian embryo and the fœtal membrane. 1. The blastodermic vesicle invested in the zona pellucida, and showing at its upper pole the embryonic area. 2. Shows the pinching off the embryo from the yolk-sac, and the formation of the amnion. 3. Further development of amnion, and commencement of allantois. 4. Completion of amnion, and growth of allantois. Chorion gives off villous processes. 5. The allantois has grown all round the vesicle, and gives off processes into the villi which are much larger than before. The yolk-sac is greatly reduced in size. *a.* Epiblast of embryo. *a'.* Epiblast of non-embryonic part of blastodermic vesicle. *al.* Allantois. *am.* Amnion. *ch.* Chorion. *ch 2.* Chorionic villi. *d.* Zona pellucida. *d'.* Processes of zona. *dd.* Embryonic hypoblast. *df.* Area vasculosa. *dg.* Yolk-stalk. *ds.* Yolk-sac. *e.* Embryo. *hh.* Pericardial cavity. *i.* Non-embryonic hypoblast. *kh.* Cavity of blastodermic vesicle. *ks.* Head-fold of amnion. *m.* Embryonic mesoblast. *n.* Non-embryonic mesoblast. *r.* Space between true and false amnion. *sh.* Chorion. *ss.* Veil-fold of amnion. *st.* Sinus terminalis. *vi.* Processes of zona pellucida. *vl.* Ventral body-wall of embryo. (KÖLLIKER.)

Development of the Nervous System.

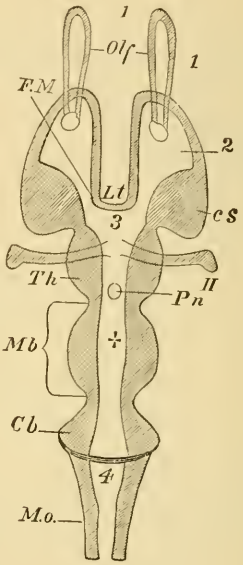
The primitive nervous system consists, as already mentioned, of a tube lying between the external blastodermic membrane and the

Fig. 563.



Primitive brain and spinal tube of man, with sixteen pairs of primitive vertebræ. The brain has divided into five bladders. *v.* Fore-brain. *z.* Twixt-brain. *m.* Mid-brain. *h.* Hind-brain. *n.* After-brain. *a.* Eye-bladders. *g.* Ear-vesicles. *c.* Heart. *dv.* Yolk-veins. *mp.* Medullary plates. *aw.* Primitive vertebræ. (Haeckel.)

Fig. 564.

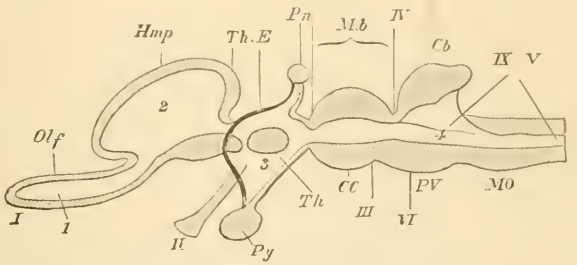


Diagrammatic horizontal section of a vertebrate brain. The figures serve both for this and the next diagram. *Mb.* Mid-brain: what lies in front of this is the fore-, and what lies behind, the hind-brain. *Lt.* Lamina terminalis. *Olf.* Olfactory lobes. *Hmp.* Hemispheres. *ThE.* Thalamencephalon. *Pn.* Pineal gland. *Py.* Pituitary body. *F.M.* Foramen of Monro. *cs.* Corpus striatum. *Th.* Optic thalamus. *CC.* Crura cerebri: the mass lying above the canal represents the corpora quadrigemina. *Cb.* Cerebellum. *I—IX.* The nine pairs of cranial nerves. 1. Olfactory ventricle. 2. Lateral ventricle. 3. Third ventricle. 4. Fourth ventricle. + Iter a tertio ad quartum ventriculum. (Huxley.)

notochord, and running from one end of the body to the other. As development advances, however, the anterior portion of the primitive neural tube separates, and subdivides into three vesicles: the anterior, middle, and posterior cerebral vesicles; while, through the further subdivision of the anterior vesicle into two, and of the posterior vesicle into two also, soon five vesicles are developed (Fig. 563), which are known, from before backward, as the prosencephalon, thalamencephalon, mesencephalon, epencephalon, and metencephalon, or as the fore-brain, between brain, mid-brain, hind-brain, and after-brain. Through the development, anteriorly and laterally, of two vesicles (Figs. 564, 565) from the anterior primary vesicle the future olfactory bulbs and optic cups are formed; while the thickening and inward growth of the walls of

the vesicles give rise to the hemispheres and the ganglia of the brain, the intervening passage-ways—that is, the remnant of the cavities of the original cerebral vesicles remaining from before

FIG. 565.



Longitudinal and vertical diagrammatic section of a vertebrate brain. Letters as before. Lamina terminalis is represented by the strong black line joining *Pn* and *Py*. (HUXLEY.)

backward as the lateral and third ventricles, the way from the third to the fourth ventricle; the cavity of the spinal portion of the primitive neural tube, persisting as the canal of the spinal cord of the adult.

CEREBRAL VESICLES AND PARTS OF BRAIN DEVELOPED OUT OF THEM.

I. Anterior, Primary, Vesicle,	1. Prosencephalon,	Cerebral hemispheres, corpora striata, corpus callosum, fornix, lateral ventricles, olfactory bulb (Rhinencephalon).
	2. Thalamencephalon (Diencephalon).	Thalami optici, Pineal gland, pituitary body, third ventricle, optic nerve (primarily).
II. Middle. Primary, Vesicle,	3. Mesencephalon,	Corpora quadrigemina, crura cerebri, aqueduct of Sylvius, optic nerve (secondarily).
III. Posterior, Primary, Vesicle,	4. Epencephalon,	Cerebellum, pons Varolii, anterior part of fourth ventricle.
	5. Metencephalon,	Medulla oblongata, fourth ventricle, auditory nerve.

At an early period of development the five different parts of the brain developed out of the primary vesicles may be more or less seen through the membranous head of the embryo. Just as we have seen, however, that through ossification of the mesoblast around and above the chorda dorsalis, the primitive spinal neural canal becomes enclosed in a bony one, the spinal column, so through the ossification of the mesoblast forming the primordial cranium surrounding the primitive cerebral vesicles, the latter, or the future brain, comes to be enclosed in a bony cavity, the skull. There are three marked differences though, to be noticed in the development of the skull, as compared with that of the spinal column. First, the notochord does not extend entirely through the head end of the em-

bryo but stops short in a tapering point at the pituitary fossa. Second, the mesoblast does not split into the skin fibrous and intestinal fibrous layers. Third, the primordial cranium never exhibits any trace of segmentation into segments or vertebræ. That the embryo skull does, nevertheless, consist of segments of modified vertebræ, though not in the sense held by Goethe,[1] the presence of visceral or branchial arches clearly proves, since the latter are morphologically cranial ribs bearing the same relation to different parts of the skull that the thoracic ribs bear to the vertebræ to which they are attached. As the primordial cranium of man, however, shows no trace of such segmentation, gives no evidence of having ever consisted of vertebræ, it is evident that the fusion or coalescence of the same must have taken place at such an early period in the development of the vertebral type that no trace of the primitive segmentation of the skull is ever seen in the transitory condition through which it passes, even in the earliest condition of the embryo. The study of the embryonic or adult skull in man will not enable us, therefore, to determine, even approximately, the number of the primitive vertebræ through the fusion of which it has been developed. The researches of Gegenbaur [2] go to show, however, that the skull of the shark retains to some extent the primordial type of segmentation, in the fact of there being eight or nine branchial arches, and that the nerves emanating from the brain, excepting the olfactory and optic, bear to the latter the same relation that the spinal nerves bear to the spinal cord. If the latter be the case, and the branchial arches be regarded as homological with so many ribs, then the primitive cranium, in the shark, at least, must have been developed through the coalescence of so many vertebræ. Returning from this brief digression upon the nature of the primordial cranium in man to the

Fig. 566.

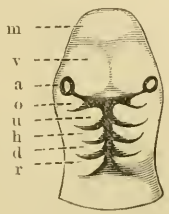
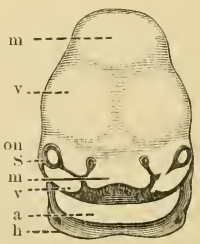


Fig. 567.



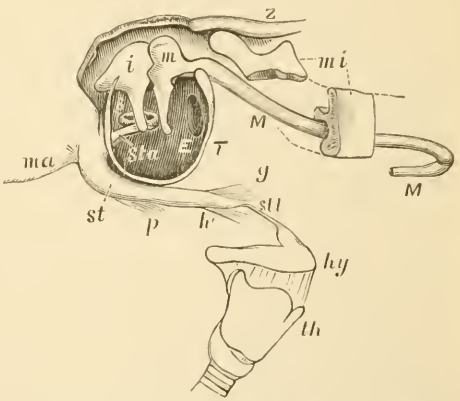
Visceral arches in man.

thread of development, let us consider what becomes of these branchial arches. The visceral or branchial arches resembling those of fishes, the intervening spaces between them being perforated by gill-like openings or slits, as in the latter animals, are four in number in man, and symmetrically disposed (Fig. 566),

[1] Virchow, Goethe als Naturforscher, 1861, s. 103.
[2] Das Kopfskelet der Selachier, 1872.

and are called from before backward the first or mandibular (u), the second or hyoid (h), the third or thyro-hyoid (d), the fourth or sub-hyoid (r) arches respectively. Through the fusion at the middle line of the distal ends of the first visceral arches (Fig. 566, u), the rudimentary lower jaw (Fig. 567, a) is developed, the permanent jaw being developed by ossification (*mi*, Fig. 568) around the cartilages of Meckel (*M*), or the rod of cartilage that early appears within this first arch, the proximal part of the cartilages of Meckel not related to the formation of the lower jaw becoming eventually the malleus (*m*) and incus (*i*) of the middle ear. It may be mentioned in this connection that the stapes is not derived from either the mandibular or hyoid cartilages, being developed as an ossification of the membrane closing the fenestra ovalis.

FIG. 568.



z. The zygomatic arch. *ma*. The mastoid process. *mi*. Portions of the lower jaw. *M*. The cartilage of Meckel of the right side, and a small part of that of the left side, joining the left cartilage at the symphysis. *T*. The tympanic ring. *m*. The malleus. *i*. The incus. *s*. The stapes. *sta*. The stapedius muscle. *st*. The styloid process. *p*, *h*, *y*. The stylo-pharyngeus, stylo-hyoid, and stylo-glossus muscles. *stl*. Stylo-hyoid ligament attached to the lesser cornu of the hyoid bone. *hy*. The hyoid bone. *th*. Thyroid cartilage. (QUAIN.)

In addition to the changes just described, there grows from the root of each of the first or mandibular arches, forward and inward, a process (Fig. 566, o), the superior maxillary, from which are developed the superior maxillary and malar bones, and a pair of cartilaginous rods which ultimately become the pterygoid plate of the sphenoid and the palate bones, which lie parallel with the trabeculæ cranii. The latter are two elongated bands of cartilage at the base of the cranium, connected with the primitive auditory capsule, which diverging to enclose the pituitary body unite beneath the anterior end of the primordial cranium to form the septum of the nose.

The basis of the cranium consists, therefore, at an early period of development, of cartilage surrounding the notochord, and continuous where the latter ends with the trabeculæ cranii, in which the basi occipital, basi sphenoid, and presphenoid bones are developed from three centers of ossification, respectively; the vault of the skull, however, with the exception of the squamo-occipital—that is, the frontal, parietal, and squamous portion of the temporal bones—being developed directly out of membrane, instead of out of cartilage. During the development of the superior maxillary process from the first or mandibular arch, as just described, there grows downward, between the primitive olfactory grooves, later, the nos-

trils, the naso-frontal process (Fig. 567, m) or the termination of that part of the investment of the head situated beneath the fore-brain (v). In this way a large cavity is formed, bounded by the naso-frontal process above, the superior maxillary process at the sides, and the primitive lower jaw below, which later, through the inward growth and coalescence of the palatine plates, is subdivided into a mouth below and a nasal cavity above, the latter being further subdivided into two by the growth of the septum nasi—the tongue growing from the inner surface of the center of the first gill arch. The second visceral arches, or hyoid arches (Fig. 566, h), growing downward, and fusing on the middle line, give rise to the lesser cornua of the hyoid bone, the stylo-hyoid ligament (Fig. 568, *stl*), and styloid process (*st*). The third visceral arches, the thyro-hyoid (Fig. 566, d), are transformed, through fusion, into the body and greater cornua of the hyoid bone. The fourth visceral arches, or the subhyoid (Fig. 566, r), do not appear to be developed into any particular organ, being situated in that part of the embryo which in the adult becomes the neck, and which is absent in the fœtus. It has just been mentioned that the branchial arches in man resemble those of fish, in that the intervening spaces are perforated by slit-like openings or clefts, through which the water passes by which the vascular gills attached to the arches are bathed and the blood aërated in the latter animals. Apart, however, from

Fig. 569.

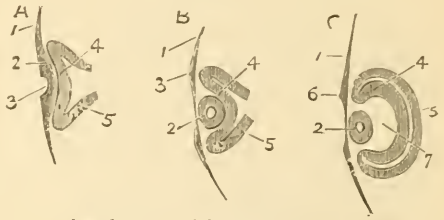
Development of the internal ear. (Haeckel.)

the fact of the branchial arches in man never being fringed with gills, as in the fish, the same present another striking difference, in that these clefts all close up, save the first one, or that intervening between the mandibular and hyoid arches, which persists as the tympano-Eustachian tube—the latter being finally, in the adult, cut off from the exterior by the growing across it of the tympanic membrane. Thus, through the transformation of the proximal ends of the first and second visceral arches, and of the cleft between them, the ear bones, meatus, tympanic membrane, tympanum, and Eustachian tube are formed, the external ear being developed from the integument near the first and second arches; the rudimentary internal ear through the invagination of that part of the epiblast situated immediately above the upper or proximal ends of the second arch, which, in time closing (Fig. 569, *A fl*, *B lc*), becomes a vesicle. The latter, the rudimentary vestibule, in giving off succes-

sively the three semicircular canals (Fig. 569, *C*, *D*, *E*, *c*, *cp*, *cst*), and the cochlea (*c*), originally a straight tube, develops into the internal ear of the adult. It will be remembered, in speaking of functions of the ear, it was mentioned that the transitory stages through which it passes in its development in man are permanently retained as such in the organ of hearing in the lower animals.

Like the ear, the eye—at least the anterior part of it—appears first as an invagination of the epiblast (Fig. 570, A, 3), which in closing up (Fig. 570, B, 2) and separating from the same gives rise to the crystalline lens (2). On the other hand, through the invagination of the optic cup or vesicle—that is, the peripheral portion of the optic nerve—by the indenting into it of the lens, the inner surface of the cup becomes the retina (4), the outer the tapetum nigrum of the choroid (5), the vitreous humor being developed through the insertion of the mesoblast from below between the lens and the retina. The remaining portions of the eye are also developed out of the mesoblast, through the latter growing around the ball of the eye as a fibrous capsule, which, splitting into an anterior and a posterior layer, gives rise to the sclerotic and cornea, and choroid and iris, respectively. Though the brain and spinal cord are developed out of the epiblast, the cranial nerves, with the exception of the olfactory and optic, which are outgrowths of the anterior cerebral vesicle, as well as the spinal nerves and sympathetic, are developed out of the mesoblast.

FIG. 570.



Development of the eye. (REMAK.)

Development of Alimentary Canal and its Appendages.

The primitive alimentary canal, like the neural canal, extending as a straight tube from one end of the body to the other, is formed, as already mentioned, through the pinching off of the internal blastodermic membrane and the intestinal fibrous layers of the middle blastodermic membrane covering it, and by the bending inward and downward of the parietes of the body, the upper portion persisting in the adult as the alimentary canal, the lower portion remaining only temporarily in the embryo as the umbilical vesicle (Fig. 571). At first the alimentary tube is closed at the ends, but as development proceeds the skin at both its extremities invaginating, deep furrows are formed, which, gradually growing

FIG. 571.

Human embryo, with umbilical vesicle; about the fifth week. (DALTON.)

toward the blind ends of the intestinal tube, finally break into the latter, and so give rise to the mouth and anus. Such being the manner in which these apertures are formed, it is evident that their lining membrane differs from that of the remaining portion of the alimentary canal in being developed out of epiblast instead of hypoblast. The mucous membrane of the mouth being then invaginated skin, the salivary glands, developed through the division and subdivision of its follicular glands, must be regarded as being essentially the same kind of glands as the sudoriparous and sebaceous glands—that is, as epidermal in origin. Hence, also, the fact of the teeth of certain fishes resembling so closely their dermal spines that at the border of the mouth it is difficult to say where the one ends and the other begins. Indeed, teeth are simply calcified mucous membrane, the invaginated oral epithelium, giving rise to the enamel, the submucous papilla below to the dentine, the pulp being made up of a matrix of connective tissue supporting blood vessels and nerve fibers.

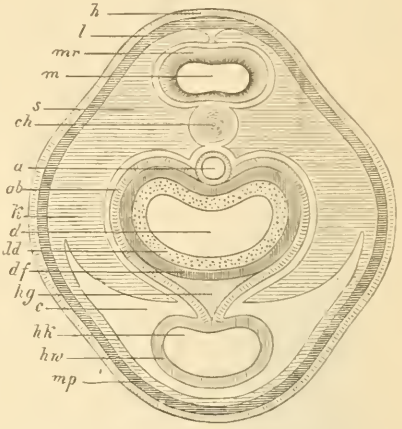
The alimentary canal does not remain long in the human embryo a simple straight tube; its abdominal portion soon expands into the stomach, while through the elongation and coiling of the part immediately succeeding the latter the small intestine is differentiated from the large one. It has been mentioned that the glandular structures of the alimentary canal are developed out of the hypoblast or its lining membrane. This is accomplished through the invagination of the latter into the wall of the alimentary canal, formed, it will be remembered, out of the intestinal fibrous layer of the mesoblast. The simple follicular glands so formed either remain as such, or, through elongation, become simple tubular glands, or, through segmentation, peptic or racemose glands. The liver and pancreas arise in a similar manner, the only essential difference being that these glands enlarge enormously and recede to a considerable extent from the alimentary canal, with which they remain, however, through life in communication through their ducts. In the case of the liver, as already mentioned, the cells, like those of the remaining alimentary canal, are hypoblastic in origin, the fibrous capsule and vessels mesoblastic, the bile ducts beginning as spaces between the cells.

Development of the Vascular System.

The heart, like the glands just mentioned, is also an appendage of the alimentary canal, but differs from the latter in being developed only out of the mesoblastic wall of the same. The heart is originally a mass of cells, but, through liquefaction of the latter, or the primitive blood corpuscles, is soon transformed into a muscular sac or tube, which remains for a short time connected by a mesentery (Fig. 572, *hg*) with the wall of the alimentary canal, of which it is, as just said, an outgrowth. Coincidently with the development of the heart, as just described, and in connection with it, there

appears, apparently through fission of the inner and outer parts of the intestinal fibrous mesoblastic wall of the alimentary canal, the two primitive aortæ and the two primitive cardinal veins, respectively. The two primitive aortæ uniting then divide again, the two branches passing along the inner surface of the first visceral arches and, curving around the anterior portion of the alimentary canal, unite anteriorly and pass as one tube into the heart. At first there are but one pair of vascular arches encircling the alimentary canal; in time, however, five such are developed (Figs. 573–576), three, however, only coexisting at one period.

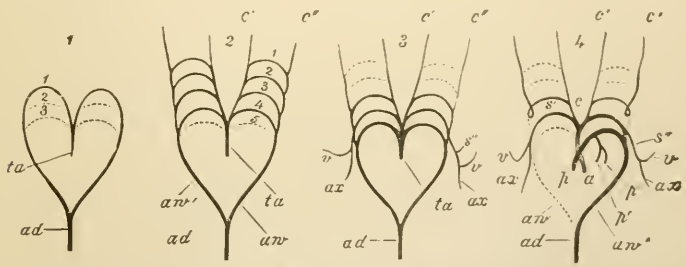
Fig. 572.



Diagrammatic transverse section through the head of an embryonic mammal. *h.* Epidermis-plate. *m.* Medullary tube (brain-bladder). *mr.* Wall of the latter. *l.* Dermis-plate. *s.* Rudimentary skull. *ch.* Notochord. *k.* Gill-arch. *mp.* Muscle-plate. *c.* Heart-cavity, anterior part of the body-cavity (*cœloma*). *d.* Intestinal tube. *dd.* Intestinal glandular layer. *df.* Intestinal muscle-plate. *hg.* Heart-mesentery. *hw.* Heart-wall. *hk.* Ventricle. *ab.* Aorta-arches. *a.* Transverse section through the aorta. (Haeckel.)

The primitive aorta further gives off lateral branches, of which two, passing to the umbilical vesicle, are known as the vitelline or omphalo-mesenteric arteries, while, through the twisting of the heart into an S-like shape, the auricles become uppermost, the ventricles lowermost. Two veins, similarly named, return from the umbilical vesicle to the body of the fœtus,

Fig. 573. Fig. 574. Fig. 575. Fig. 576.

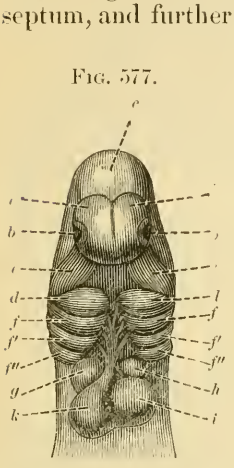


Metamorphosis of the five arterial arches in the human embryo. *ta.* Arterial stalk. 1, 2, 3, 4, 5. The arterial arches from the first to the fifth pair. *ad.* Main stem of the aorta. *au.* Roots of the aorta. In Fig. 573, three of the arterial arches are given: in Fig. 574, the whole five (those indicated by dots are not yet developed); in Fig. 575, the first two have again disappeared; in Fig. 576, the permanent arterial stems are represented. The dotted parts disappear. *s.* Subclavian artery. *v.* Vertebral artery. *ax.* Axillary artery. *c.* Carotid artery (*c'*, outer; *c''*, inner carotid). *p.* Pulmonary artery (lung-artery). (Rathke.)

and pass as a single trunk, the sinus venosus, into the heart. Such being the disposition of the heart and the primitive vessels, it follows that the nutritive material of the umbilical vesicle passes by the

vitelline veins to the heart, and thence through the vascular arches to the primitive aorta and so to the body generally, the circulation being completed by the vitelline arteries. Neither the heart, aortic trunk, nor vascular arches remain, however, long in the condition in which they have just been described. The heart soon subdivides into a right and left heart through the growth of a longitudinal septum, and further into auricles and ventricles (Fig. 577) through the growth of transverse septa, the septum between the auricles remaining, however, incomplete until after birth, the opening so caused being known as the foramen ovale. Coincidently with the development of the cavities of the heart through the growth of a longitudinal septum in the common arterial trunk, the latter subdivides into aorta and pulmonary artery, the aorta finally being disposed to the right, the pulmonary artery to the left. Finally through the transformation of the third, fourth, and fifth vascular aortic arches, the first and second having disappeared, the aorta and its first main branches and the pulmonary artery are developed, the change being brought about through the atrophy or hypertrophy of these arches respectively. Thus, for example (Figs. 573–576), of the left fifth arch (5), the internal half becomes the pulmonary artery (*p*), the external half the ductus arteriosus, the right fifth arch disappearing.[1] The left fourth arch (4) becomes the permanent aorta and gives off the left subclavian artery (*s*). The right fourth arch develops into the innominate dividing into the right subclavian and right common carotid, the left common carotid being given off by the aorta. The third left arch (3) on both sides enters more into the formation of the internal carotid than of the external one, its outer connecting portion, as well as that of the fourth arch, disappearing.

Fig. 577.



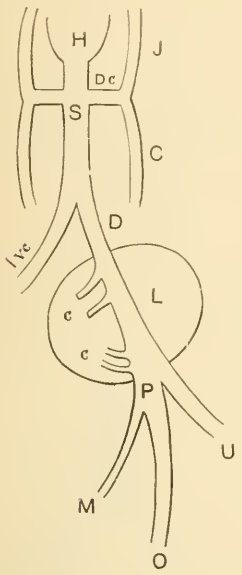
Heart and head of an embryonic dog, from the front. *a*. Fore-brain. *b*. Eyes. *c*. Mid-brain. *d*. Primitive lower jaw. *e*. Primitive upper jaw. *ff'*. Gill-arches. *g*. Right auricle. *h*. Left auricle. *i*. Left ventricle. *k*. Right ventricle. (Bischoff.)

With the establishing of the allantois, however, and the dwindling away of the umbilical vesicle, the allantoic or second circulation gradually replaces the vitelline or first one. The allantoic or umbilical veins, originally two in number, appear to be developed as branches of the vitelline veins, which, extending themselves through the allantois, finally pass into the villous processes of the chorion. Shortly after the appearance of the umbilical veins, the right one disappears, and with it the right vitelline vein and that part of the left vitelline outside of the body of the embryo. The mesenteric portion of the latter, or left omphalo-mesenteric vein (Fig. 578, M), enlarges, however, while the remaining portion (O),

[1] The embryo is supposed to be lying upon its dorsal surface.

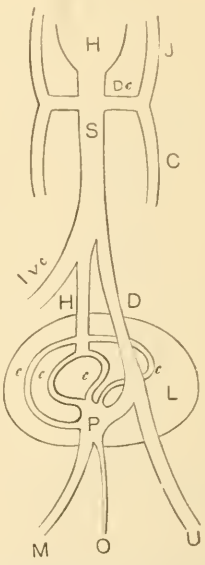
that returning from the umbilical vesicle, atrophies. At the same time the left umbilical vein (Fig. 578, U) becomes very much enlarged, and as it is a branch of the omphalo-mesenteric vein it will,

Fig. 578.



Diagrammatic view of portal and umbilical circulations.

Fig. 579.

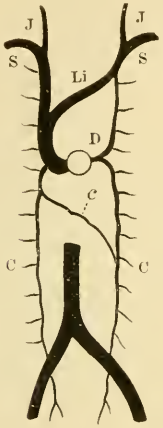


Diagrammatic view of portal and umbilical circulations more advanced.

with the mesenteric branch of the same, pass as one trunk (P D) to the sinus venosus (S), and so reach the heart (H). The continuity, however, of this trunk due to the union of the umbilical and omphalo-mesenteric vein is interrupted by the development of the liver (L) as an investing mass around it, and by the appearance of the inferior vena cava. The latter may be regarded as the backward prolongation of the sinus venosus (S), and in dividing posteriorly into two branches gives rise to the two iliac veins. With the growth of the liver the common trunk (Fig. 579, P), which may now be called the portal vein, gives off capillaries (C C), which, ramifying through the liver, pass into the vena cava by a distinct vessel, the hepatic vein (Fig. 579, H). The amount of blood circulating through the hepatic capillaries (*c c*) at this period is, however, but small, since little blood comes from the intestines through the mesenteric vessel (M), while of the blood passing through the umbilical vein (U) the greater part flows directly through what may be now called the ductus venosus (D) into the inferior vena (Ivc), very little mixing with the blood of the portal vein (P). It will be remembered that the single aorta formed through the union of the vascular or branchial arches, passing from the heart along the inner surface of the visceral arches, soon divides into the two

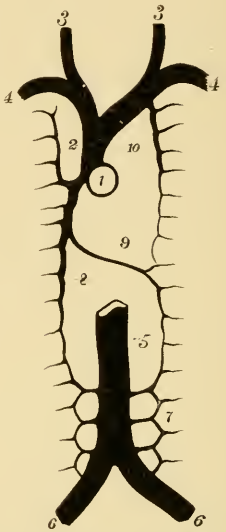
primitive aortæ that run along toward the posterior end of the body on either side of the notochord. As development proceeds, the point of division of the aorta is carried much further back, its two branches becoming the iliac arteries.

Fig. 580.



Further development of the venous system. The cardinal veins (C) are diminished in size. The canal of Cuvier (D) on left side much atrophied. Primitive left innominate vein (Li), and primitive vena azygos minor vein (*c*) appearing. J. Jugular vein. S. Subclavian vein. (Dalton.)

Fig. 581.



Adult condition of venous system. 1. Right auricle of heart. 2. Vena cava superior. 3, 3. Jugular veins. 4, 4. Subclavian veins. 5. Vena cava inferior. 6, 6. Iliac veins. 7. Lumbar veins. 8. Vena azygos major. 9. Vena azygos minor. 10. Superior intercostal vein. (Dalton.)

From the internal part of the latter, that which becomes later the internal iliac arteries, two vessels are given off, which, passing to the allantois, give rise to the umbilical or hypogastric arteries. In the meantime the primitive cardinal veins (Fig. 580, C C), uniting with the jugular veins (J J), pass into the sinus venosus, and so to the heart, there being at this period then two superior venæ cavæ, a disposition which is retained during life in the elephant, manatee, rodents, monotremes, and birds. This condition, however, is only a transitory one, since a vessel (Li, Fig. 580) is given off from the point of union of the left jugular and subclavian veins, which, uniting with the corresponding vessel of the right side, forms the superior vena cava (2, Fig. 581), the left primitive superior vena cava almost entirely disappearing, being only represented in the adult by the coronary sinus and a fibrous band descending obliquely on the left auricle. Such being the disposition of the venous system with the establishment of the allantois, or, as we shall see presently, of the placenta, the heart in the meantime having become four-chambered, the allantoic

or second circulation will be as follows: The blood returning from the head and upper extremities will pass to the right auricle of the heart by the superior vena cava, thence by the right ventricle and ductus arteriosus to the aorta, and so to the lower extremities, and to the allantois by the umbilical arteries. The latter being nourished by blood that has circulated through the head, etc., will be relatively, therefore, poorly nourished. On the other hand, the blood of the umbilical vein returning directly from the allantois or placenta laden with nutritive material and oxygen absorbed from the maternal blood will pass with little or no admixture from the portal blood into the right auricle, whence guided by the Eustachian valve it will pass through the foramen ovale into the left auricle, thence into the left ventricle, and so by the aorta to the head, hence the fact of the latter being so much better developed than the rest of the body. But little blood passes through the lungs in the fœtus, aëration being effected by the placenta; on the other hand, a very large amount traverses the liver, which may be accounted for on the supposition that the liver acts as a decarbonizer of the blood, supplementing in this way the want of action of the lungs. At all events, with the establishing of the pulmonary respiration, the liver becomes smaller, relatively, while in animals, generally, the lungs and liver are in an inverse ratio as regards size and functional importance. With the replacing of the second or allantoic circulation by the adult pulmonic and systemic circulations the foramen ovale closes, the ductus arteriosus, umbilical vein, and umbilical arteries being shrivelled up into cords. The internal portion of the latter remains, however, pervious, and persists in the adult as the superior vesical arteries, while the part of the allantois remaining within the body becomes the urinary bladder and urachus.

Development of Respiratory Organs.

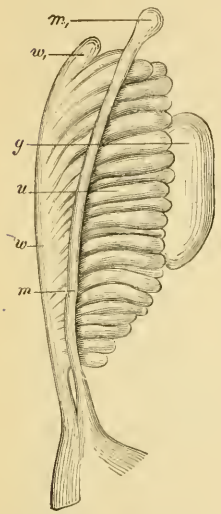
The respiratory organs may be regarded as appendages of the alimentary canal, since the trachea and œsophagus are originally one and the same tube. As development advances, the trachea separates itself from the œsophagus, the upper portion becoming the larynx, the lower subdividing into the two bronchi, the latter, by a process of fission and segmentation, giving rise to the bronchial tubes and pulmonary lobules.

Development of the Genito-urinary Organs.

The genito-urinary organs are so intimately associated in their development that it will be found convenient to study them together. In describing the structure of the kidney, it was mentioned that, however complex in structure the organ may appear to be, it consists essentially of a tube open at one end, from which are given off diverticula terminating in blind globular-like expansions.

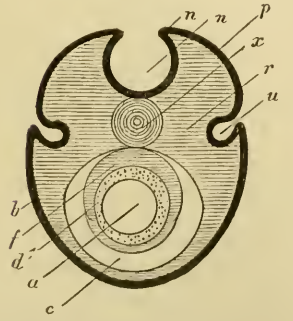
Such a primitive type of structure is presented through life in the kidneys of the myxinoid fishes, and as a transitory condition in man in the early period of development. The common duct (Fig. 582, *w*), running from end to end of the body on either side of the notochord, which gives off the primitive urine tubes (Fig. 582, *u*), is known as the Wolffian duct and appears to be developed out of the skin sensory layer (583, *u*) by invagination and constriction, precisely as the spinal cord is developed, the duct, however, receding (Fig. 584, *u*) farther from the general surface of the body than the cord, and terminating in the cloaca or lower portion of the alimentary canal. Coincidently with the development of the Wolffian duct and its diverticula, or the primitive kidneys, there appears in the mesoblast just at that part where the latter splits into the intestinal fibrous layer (Fig. 584, *d*), and the skin fibrous layer (*h f*), the so-called indifferent gland, the cells of which differ in many respects from those of which the latter layers consist, and out of which the germinal epithelium (Fig. 585, *g*) giving rise to either ova or spermatozoa, as the case may be, appears to be developed. Such a condition of the urinary apparatus does not, however, remain long, there being developed out of the posterior portion of the Wolffian duct near where it passes into the cloaca a secondary duct, the primitive ureter, which gradually

Fig. 582.



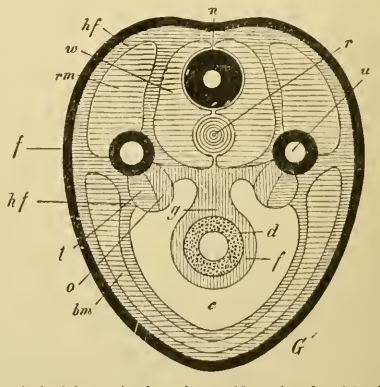
Primitive kidney of a human embryo: *u*. The urine tubes of the primitive kidney. *w*. Wolffian duct. *w'*. Upper end of the latter (Morgagni's hydatid). *m*. Müllerian duct. *m'*. Upper of the latter (Fallopian hydatid). *g*. Hermaphrodite gland, becoming either testicle or ovary. (Kobelt.)

Fig. 583.



b. Skin sensory layer. *n*. Spinal tube. *u*. Beginning of Wolffian body. *x*. Notochord. *c*. Body cavity. *f*. Intestinal fibrous layer. *d*. Intestinal glandular layer. *a*. Intestinal tube. (Haeckel.)

Fig. 584.

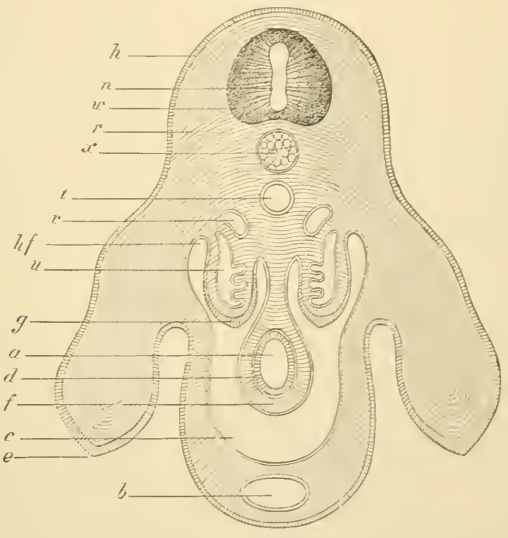


n. Primitive spinal cord. *r*. Notochord. *hf*. Skin fibrous layer. *w*. Vertebræ. *f*. Skin sensory layer. *rm*. Dorsal muscles. *bm*. Ventral muscles. *g*. Mesentery. *to*. Indifferent sexual gland. *d*. Intestinal fibrous layer. *f*. Intestinal glandular layer (Haeckel.)

elongates and gives off diverticula, which become the renal tubules, and disposed with reference to the blood vessels precisely as the diverticula of the Wolffian duct were. The urine excreted by the former, however, passes into the posterior part of the stalk of the allantois, or the urachus, which, dilating, is retained in the body as the primitive bladder. The latter in time separates both from the cloaca and that part of the allantois which comes away as the umbilical cord and the fœtal portion of the placenta.

In this manner the permanent kidneys grow out of and replace the primitive ones developed out of the Wolffian duct. The latter,

FIG. 585.



Transverse section through the pelvic region and the hind limbs of a chick on the fourth day of incubation (about forty times the natural size). *h.* Skin sensory layer. *w.* Medullary tube. *n.* Spinal canal. *u.* Wolffian body or primitive kidneys. *x.* Chorda. *v.* Hind limbs. *b.* Allantois canal in the ventral wall. *t.* Aorta. *r.* Cardinal veins. *a.* Intestine. *d.* Intestinal-glandular layer. *f.* Intestinal fibrous layer. *hf.* Skin muscle layer. *g.* Germ-epithelium. *x.* Dorsal muscles. *c.* Body cavity (*coloma*). (WALDEYER.)

however, do not disappear, but split (Fig. 586) into two distinct tubes, the outer still called the Wolffian duct (*w*), the inner the Müllerian duct (*m*). The Wolffian duct, as just mentioned, for a time carries off the urine excreted by its tubules from the blood, but, as this office is transferred to the ureter and permanent kidneys, it gradually is transformed, if the individual becomes a male, into the epididymis and vas deferens, and will hereafter carry to the urethra the spermatozoa developed by the hitherto indifferent body (*ot*), now, therefore, a testicle; the Müllerian ducts, at their lower distal united portion, persisting as the sinus pocularis, the homologue of the vagina; the upper proximal portions as the so-called hydatid of Morgagni. On the other hand, if the individual becomes a

female, the gland (*ot*) produces eggs, and is henceforth, therefore, an ovary. The Müllerian ducts fuse together from below upward and become the vagina, uterus, and Fallopian tubes; the Wolffian ducts persisting in an atrophied condition, in the human female, as the parovarium, or the white tortuous tubes in the broad ligament of the uterus; and in that of certain animals, the pig, as the ducts of Gaertner opening into the vagina. At an early period of intrauterine life the conjoined Wolffian and Müllerian ducts pass as the genital cord (Fig. 586, *gc*) into the expanded stalk of the allantois, or urogenital sinus (*ug*); the latter, in time, emptying, together with the alimentary canal (*i*), into the cloaca (*cl*), or cavity common to both. As development advances, however, the rectum separates from the cloaca, and if the individual becomes a female a further differentiation takes place, in that the lower united portion of the Müllerian ducts, or the vagina, terminates in an opening distinct from that of the urethra, or the passage-way from the bladder. The latter, in the case of the individual being a female, will pass beneath the clitoris, or female penis, the two adjacent folds of skin becoming the labia minora, the two lateral external ones the labia majora, the ovaries lying within, in the body cavity. On the other hand, if the individual be a male, the urethra passes through the elongated penis; the under-skin of which is formed by the coalescence in the middle line of what, in the female, constitute the labia minora; the scrotum being formed through the fusion along the future raphe of the parts corresponding to the labia majora, into which the testicles descend by passing through the inguinal canal, the peritoneum consequently pushed in front of them becoming the tunica vaginalis testis. Such being the manner in which the external generative organs are developed in the two sexes, it will be readily understood why, in those male individuals, on the one hand, in which development is arrested at the stage at which the external generative organs in the two sexes are alike; and in the

Fig. 586.

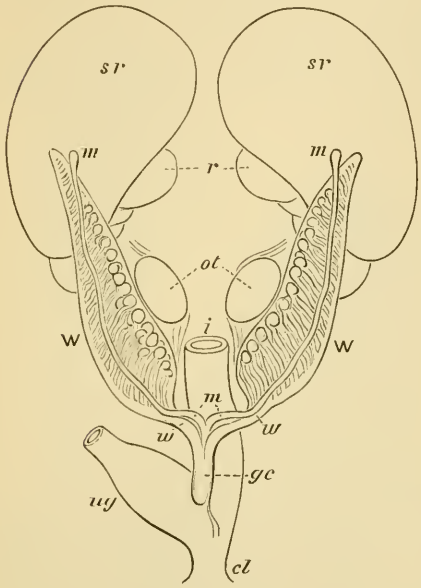


Diagram of the Wolffian bodies, Müllerian ducts, and adjacent parts previous to sexual distinction, as seen from before. *sr*. The suprarenal bodies. *r*. The kidneys. *ot*. Common blastema of ovaries or testicles. W. Wolffian bodies. *w*. Wolffian ducts. *m*, *m*. Müllerian ducts. *gc*. Genital cord. *ug*. Sinus urogenitalis. *i*. Intestine. *cl*. Cloaca. (Quain.)

other, in those female ones in which the clitoris is much elongated, that such should be regarded by the vulgar as hermaphrodites, though in neither case is hermaphroditism really present. Bearing in mind what has just been said as to the development of the uterine generative organs, it is readily conceivable, also, that if one of the indifferent bodies of early intra-uterine life became a testicle, and the other an ovary, and both functionally active, or if two ovaries and two testicles were developed through the subdivision of the indifferent bodies, which consisted, probably, of both male and female elements; and further, that the Wolffian ducts became vasa deferentia, and the Müllerian ducts the vagina, uterus, and Fallopian tube or tubes; that the same individual might produce ova and spermatozoa, and that an egg might be developed in the uterus of the individual producing it after fecundation by its own spermatozoa, or by those of a similar or normal male individual. In such a hypothetical case there would be, however, either a penis or clitoris, but not both, and either a scrotum or labia majora, but not both. While a condition, like that just described, is, therefore, within the limits of possibility, it is extremely doubtful whether such a case ever actually existed in a human being, though hermaphroditism obtains in many of the lower animals, mollusca, worms, etc., and in numerous plants; the stamens and pistil of a flower constituting the male and female generative organs respectively. The only true test of sex being the power of producing ova or spermatozoa, it is obvious that however much the external or internal organs in any one individual may resemble those of the normal male or female as due to either hypertrophy or arrest of development, that such modified organs cannot be taken alone as an evidence of sex.

Development of Extremities.

The limbs first appear as bud-like protuberances from the sides of the body (Fig. 585, *c*), those giving rise to the upper extremities being developed first. While covered by the outer or skin sensory layer, the limbs are developed more especially out of the deeper or skin fibrous layer, through its cells becoming first cartilage, with after-ossification of the same. As development advances, the primitive limb-bud recedes from the body, and expanding at its distal extremity, segments the divisions so arising, becoming, hereafter, the fingers and toes—the characteristic bones with the correlated muscles being gradually developed in the same.

Résumé of Development of Fœtus.

On the supposition that the ontogeny or development of the individual is the epitomized phylogeny or history of the race, we have some explanation of the fact that the various changes through which the embryo passes represent morphologically the permanent condition of lower forms of life. The principal changes undergone

by the embryo during its development, which we have just endeavored to describe and account for, may be synoptically resumed about, as follows:

At the twelfth day, the ovum, about 5 millimeters ($\frac{1}{5}$ of an inch) in length, consists of the zone pellucida beset with small villi, and enclosing a two-layered vesicle, the blastodermic vesicle.

At the fifteenth day the embryo, about 2 millimeters (the $\frac{1}{12}$ of an inch) in length, exhibits the primitive groove, amnion, allantois, and umbilical vesicles; the heart, though still one-chambered, is present, and the first or vitelline circulation is established, and the rudiments of the Wolffian duct indicated.

At the twentieth day the embryo, about 3 millimeters ($\frac{1}{8}$ of an inch) in length, presents the visceral arches and perforated clefts.

At the twenty-first day the embryo, about 4 millimeters ($\frac{1}{6}$ of an inch) in length, has developed rudimentary eyes, ears, mouth, three cerebral vesicles, and the heart has become four-chambered.

At the end of the first month the embryo has attained a size of 12 millimeters ($\frac{1}{2}$ an inch), and is characterized by the presence of distinct rudimentary limbs, the whole ovum measuring about 17 millimeters.

At the end of the second month the embryo is about 25 millimeters (1 inch) in length, and weighs about 4 grammes ($\frac{1}{8}$ of an ounce), the whole ovum measuring about 7 centimeters (2.4 inches). By this time the vitelline vessels and right umbilical vein are obliterated, the future fingers and toes are indicated, the outer ear has appeared, nose and eyelids are present; the umbilical cord is about 16 millimeters ($\frac{2}{3}$ of an inch) in length, and ossification has begun in the lower jaw, clavicle, ribs, vertebral bodies; permanent kidneys present, but sex still indistinct.

At the third month the fœtus is about 10 centimeters (4 inches) in length, weighs about 20 grammes ($\frac{2}{3}$ of an ounce); a difference of sex is indicated by the external genitals, the umbilical cord is 7 centimeters (2.8 inches), and the placenta begins to be formed.

At the fourth month the fœtus is 17 centimeters (7 inches) long, weighs 120 grammes (4 ounces); umbilical cord is 19 centimeters (7 inches) long, and weighs 80 grammes (2.6 ounces).

At the fifth month the fœtus is about 20 centimeters (8 inches) in length, and weighs 284 grammes (9 ounces); the hair of the head and of the body, or lanigo, is quite distinct, and covered with the vernix caseosa; the umbilical cord is about 31 centimeters (12 inches) long, and the placenta weighs 178 grammes (6 ounces).

At the sixth month the fœtus is 28 centimeters (11 inches) long, and weighs 634 grammes (20 ounces), and meconium appears in the intestines.

At the seventh month the fœtus is about 35 centimeters (14 inches) long, and weighs 1,218 grammes ($2\frac{1}{2}$ pounds); the eyes are open, one testicle has descended into the inguinal canal, and, if born at this period, is viable.

At the eighth month the fœtus is 42 centimeters (16 inches) in length, and weighs between 1 and 2 kilos. (2.2 to 4.4 pounds); one testicle has descended into the scrotum.

At the end of the ninth month, or at full term, the fœtus is about 51 centimeters (20 inches) in length, and weighs 3¼ kilos. (7 pounds).

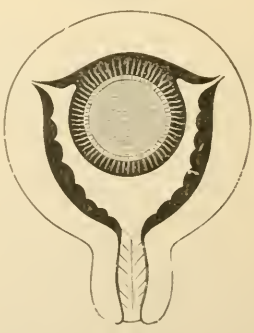
Development of the Placenta.

Up to the present moment nothing has been said as to the changes undergone by the mucous membrane of the uterus after the ovum impregnated has passed into the cavity of the same. These changes, which must now be at least briefly considered, appear to differ rather in degree than in kind from those exhibited by the mucous membrane during menstruation, the essential difference being that the mucous membrane during pregnancy is hypertrophied to a far greater extent, and more of it is finally cast off than during menstruation. As the fecundated egg passes through the Fallopian tube, the mucous membrane of the uterus becomes tumefied, vascular, and rugose, projecting as rounded eminences into the cavity of the uterus (Fig. 587), the uterine tubules at the same time elon-

Fig. 587.

Impregnated uterus, with projecting folds of decidua growing up around the egg. The narrow opening, where the edges of the folds approach each other, is seen over the most prominent portion of the egg. (Dalton.)

Fig. 588.



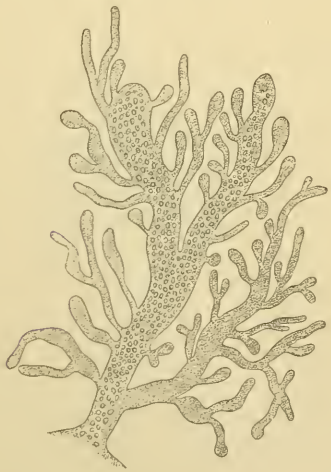
Impregnated uterus: showing connection between villosities of chorion and decidual membrane. (Dalton.)

gating and expanding to such an extent that their open mouths become perceptible at the surface. The mucous membrane so modified is a thick, soft, velvety, vascular lining, quite different from that of the unimpregnated condition; indeed, so much so that the decidua vera, as the membrane is now called, was supposed at one time to be of new formation.

The decidua vera is, however, only the hypertrophied mucous membrane of the uterus, its cells being derived from the connective tissue cells of the latter, and is continuous at the orifices of the Fallopian tubes with the mucous membrane lining the latter, and at the os internum with that lining the cervix. It should also be

mentioned that at this period the cavity of the latter becomes so filled with a viscid-like mucus that the passage-way to the vagina is blocked up, the ovum within the cavity of the uterus being thereby protected from external influences. The impregnated egg having reached the uterine orifice of the Fallopian tube, passes through the latter into the cavity of the uterus and is caught, as it were, between a pair of the folds of the decidua vera, and retained there by the growing downward and around of the latter until the ovum is completely inclosed by the same. The reflected folds so developed are known as the decidua reflexa (Fig. 588), that portion of the decidua vera lying between the ovum and the wall of the uterus as the decidua serotina. It has already been mentioned that the chorion or vitelline membrane of the ovum at an early period of intrauterine life is covered with small villous-like processes, which in time become vascular through being penetrated by the blood vessels of the allantois. The villi, when examined by the microscope (Fig. 589), present such a very characteristic ap-

Fig. 589.



Compound villosity of human chorion, ramified extremity. From a three months' fœtus. Magnified thirty diameters. (Dalton.)

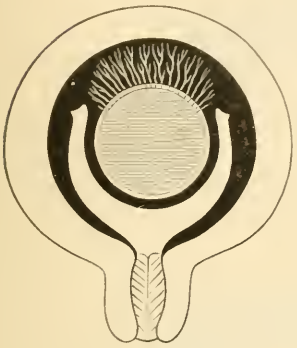
Fig. 590.

Extremity of villosity of chorion, more highly magnified; showing the arrangement of blood vessels in its interior. (Dalton.)

pearance that their presence may be accepted as positive proof of the existence of a fœtus, as much so, indeed, as if the fœtus itself had been found. The general appearance of a villus is like that of a seaweed, originating in the chorion by a trunk, which divides and subdivides into filamentous branches, swollen here and there and terminating in rounded extremities, and consisting internally of a finely granular substance containing nuclei. At first the villous processes of the chorion are without vessels, but with the establishment of the allantois they become vascular through

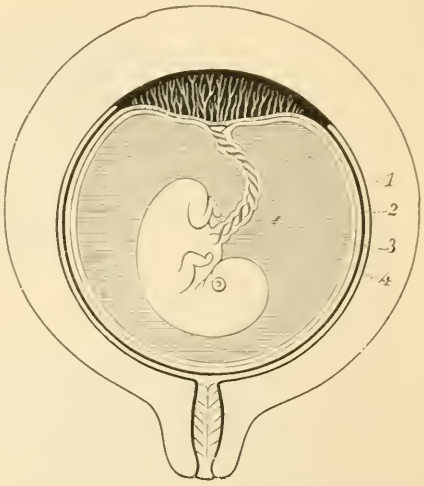
prolongation of the terminal allantoic vessels, which (Fig. 590) are disposed in loops. As development advances, however, the chorion loses its villi, except at that part of it in contact with the decidua serotina (Fig. 591), but here the villi are much developed, dividing

Fig. 591.



Pregnant uterus: showing the formation of the placenta by the local development of the decidua and the chorion. (Dalton.)

Fig. 592.



Pregnant human uterus and its contents, about the end of the seventh month: showing the relations of the cord, placenta and membrane. 1. Decidua vera. 2. Decidua reflexa. 3. Chorion. 4. Amnion. (Dalton.)

and subdividing and insinuating themselves as they grow into the mucous membrane or decidua serotina of the uterus. The latter in the meantime hypertrophies, grows downward, around, and between the villous processes of the chorion (Figs. 593, 594, *v*), its capillaries (*vc*) at the same time becoming enormously dilated, being finally transformed into sinuses into and from which pass a uterine artery (*ua*) and vein (*uv*). The wall of the sinus eventually fusing with that of the villous process of the chorion (*v*), and the latter with the wall of the capillary, eventually the maternal blood in the sinus (*vc*) is separated from the fœtal blood in the villous process (*fc*) by a membrane so thin as not to exceed the $\frac{1}{1600}$ of a millimeter ($\frac{1}{40000}$ inch) in thickness, which readily permits of the osmosis of nutritive materials and oxygen from the mother's blood into that of the fœtus, and of effete materials from the blood of the fœtus into that of the mother, though at no time is there any connection between maternal and fœtal vessels. The organ so formed, with nutritive and respiratory functions, is called the placenta, and evidently consists of two parts, fœtal and maternal, the allantois and decidua serotina, which, however, become so intimately united that eventually they are inseparable, and are cast off as such during labor as the "after-birth." As development proceeds, the amnion becoming distended

with the fluid given off by the fœtus, consisting principally of water, some urea and alkaline salts, comes in contact about the fifth month of pregnancy with the chorion and adheres more or less to the latter by a gelatinous layer of tissue, the tunica media of Bischoff.

Fig. 593.

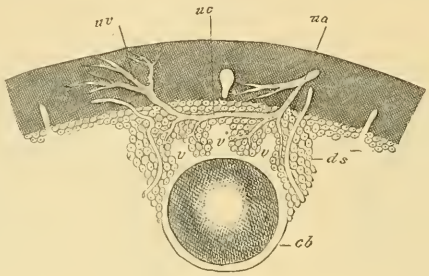


Fig. 594.

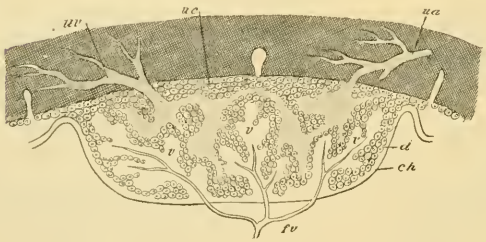
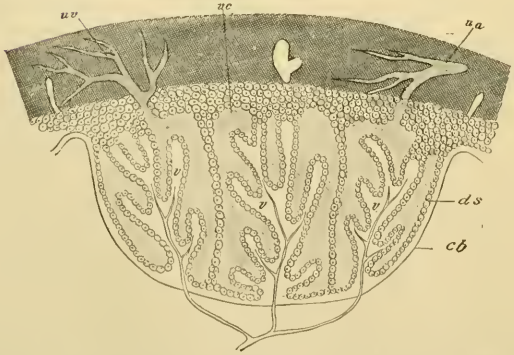


Fig. 595.



ua. Uterine artery. *uc.* Uterine capillary. *uv.* Uterine vein. *ds.* Decidua serotina. *ch.* Chorion. *v.* Villous processes of chorion. *fv.* Fœtal vessels. (Ercolani.)

The decidua reflexa, fusing in turn, about the seventh month of pregnancy with the decidua vera,[1] it so comes that at the end of

[1] It should be mentioned, however, that according to many embryologists the decidua reflexa begins to atrophy about the fifth month of gestation, and being gradually absorbed finally disappears between the sixth and seventh months.

pregnancy the fœtus, suspended from the placenta by the umbilical cord, floats in the amniotic fluid, the enclosing sac of which consists of the layers just mentioned.

With the rupture of the latter and the escape of the water, etc., the child is born, and that life begins which it has been the object of this work to endeavor to describe.

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